THE CLASSIFICATION OF THE ANOMALONINAE (HYMENOPTERA : ICHNEUMONIDAE)

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CONTENTS

SYNOPSIS

A revised classification is proposed for the Anomaloninae on the basis of the genitalia (particularly those of the male) and various external characters, often previously unused. A hundred characters were examined in each type-species and an average linkage dendrogram has been constructed from the resulting similarity matrix. All the genera and subgenera are redefined and their interrelationships discussed. Two tribes and 35 genera, of which two are new, are recognized as valid. Two genera are divided into subgenera, two of which are new. Four previously unknown final instar larvae and a first instar larva are described. Keys are given to genera and subgenera, both for adults and for described final instar larvae.

INTRODUCTION

The Anomaloninae are a large group of quite uncommon Ichneumonids which are distributed throughout all major zoogeographical regions of the world. Many species occur in afforested areas where they parasitize the larvae of a number of economically important insects. The majority of Anomaloninae are parasites of lepidopterous larvae, usually ovipositing in early instars and with the adult parasites emerging from the host pupa. One small tribe, the Anomalonini, are parasitic upon Tenebrionid larvae.

Adult Anomaloninae have been reared from a variety of hosts and individual species do not appear to be particularly host specific. For instance, *Agrypon flaveolatum* has been reared from pupae belonging to eight different families of Lepidoptera. There is evidence to suggest that it is the habitat preference of these insects which is the major limiting factor in their distribution (Townes, 1958; 1962; Gauld, 1973*b*) and that within any one particular habitat type they will oviposit into any suitable lepidopterous larvae.

During the study of the Anomaloninae it became increasingly obvious that the limits of many genera are poorly defined and, in consequence, difficulty is experienced in placing some species. By the examination of type-species and a number of other species which are referred to the various genera, it has been possible to define the genera. This part of the work (1968–1971) was duplicating that done by Townes (1971). Subsequent and more detailed study of this material and large numbers of undescribed species have necessitated the alteration of generic limits. Emphasis has been placed on previously unused characters and special attention has been paid to the structure of the genitalia, particularly that of the male. The structure

of the male genitalia is in many cases characteristic of the various taxa. In the past many authors used differences in wing venation to facilitate generic separation. As there is considerable variation in the venation, even within a species, the more general descriptive form taken by these authors may prove unreliable. Measurement of the wings has enabled these characters to be quantified. By studying inter- and intra-generic variation it has been possible to relate species groups together, place several otherwise unplaced species and produce generic diagnoses that not only include many new characters, but outline variation occurring in other characters and discard some features as of little use for effecting generic separation.

Terminology in this work follows that of Richards (1956) except that the naming of wing cells follows the system proposed by Eady (1974). Terminology for larval structure follows that of Short (1959) and for the male genitalia that of Peck (1937). Where any confusion about the terminology employed could occur labelled figures are included. The description of microsculpture follows the nomenclature proposed by Eady (1968).

Certain points concerning the terminology of morphological structures must be mentioned here. The flagellum is defined as that part of the antenna distal to and not including the reduced third antennal segment, the anellus. The term mesoscutum is used for the large dorsal thoracic sclerite and not mesonotum. The definitive mesonotum includes the scutellum and the prescutum, which in Ichneumonidae is extremely reduced (Compere & Rosen, 1970). The term meso-

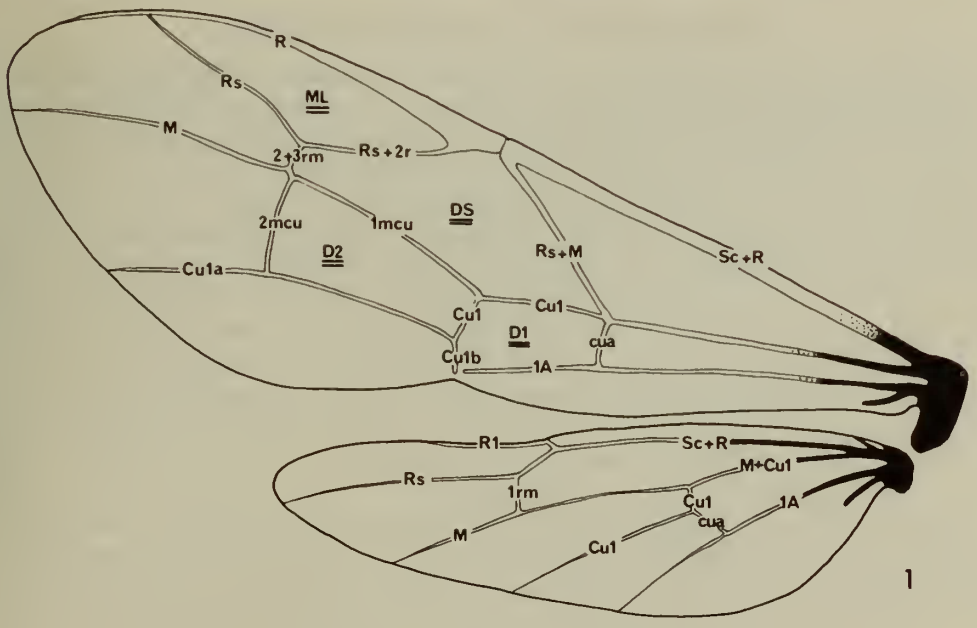

FIG. 1. Left fore- and hindwings of *Habronyx* (*Habronyx*) *heros* (Wesmael) labelled to show venation and wing cells. Abbreviations used for wing cells: ML marginal cell; DS discosubmarginal cell; D1 first subdiscal cell; D2 second discal cell.

sternum is used when referring to the ventral region of the mesothorax, although it is not certain that this area is the definitive mesosternum. The propodeum (which corresponds to the 'metathorax' of Morley, 1915 and Schmiedeknecht, 1936) is the original 1st segment of the abdomen. The remainder of the abdomen is termed the gaster. When referring to a particular tergite of the gaster, e.g. tergite 2, the number indicates the gastral, not abdominal, segment number.

The nomenclature of certain veins in the wings of Ichneumonidae is not wholly resolved. Some workers (Schmiedeknecht, 1936; Smith & Shenefelt, 1955; Townes, 1969) have used a derived Jurinian system for naming of veins. This system has many advantages, but in the present work the naming of veins follows the Richards (1956) interpretation of the Comstock-Needham system (Text-fig. 1). In the Anomaloninae only a single intercubital (*rm*) vein is present. This vein has variously been called either *2rm* or *3rm*, depending upon its position in relation to *2m–cu*. However, within a single species (*Habronyx heros*) *rm* has been found to be distal, opposite or proximal to *2m–cu*. Therefore to call this vein either *2rm* or *3rm*, depending upon its relative position, is to unjustifiably emphasize the importance of its position and to infer that in two specimens (with *rm* differentially placed in respect to *2m–cu*) the intercubital veins are not homologous. In many subfamilies that are possibly closely related to the Anomaloninae there is fusion apically between *2rm* and *3rm*. It is considered possible that within the Anomaloninae the intercubital vein may be *2* + *3rm* and this designation is used in the present work.

REVIEW OF THE PREVIOUS WORK

Prior to 1960 authors included the Anomaloninae within the subfamily Ophioninae as two separate tribes, the Anomalonini (which they called the Nototrachini) and the Therionini (which they called the Anomalini). This change in the position of the name Anomalonini has resulted from confusion over the use of the generic name *Anomalon* (see p. 85). The family-group name Anomaloidea was first used for the Ichneumonidae by Foerster (1868) but subsequent authors (Ashmead, 1901*a*; Schmiedeknecht, 1936) amended this to Anomalonini. Townes (1971) uses the names Anomalinae and Anomalini, thus reverting to the original Anomal- stem. However, Anomalitae was first used as a family group name in the Coleoptera (to include *Anomala* Samouelle) in 1850. Therefore under Article 55 of the *International Code of Zoological Nomenclature* the family-group name Anomalinae in the Ichneumonidae becomes a junior homonym. The amended form, Anomaloninae, which is already widely used amongst European workers would therefore appear to be the most suitable name for this subfamily.

In recent years the classification of the Ichneumonidae has undergone considerable modification. The subfamily Ophioninae of classical authors has been divided into a number of discrete subfamilies (Townes, 1969). Some modern authors (Short, 1959; Townes *et al.*, 1965) have combined the Therionini with the Anomalonini and elevated the resultant combination to the rank of a subfamily, the Anomaloninae.

Viktorov (1968) discussed the position of the Therionini at some length and

concluded by suggesting that these insects should be retained in the Ophioninae as a tribe. This system of classification had been adopted by Aubert (1966), Smith & Shenefelt (1955) and Perkins (1959).

Short (1959) noted a marked degree of similarity in the structure of the cephalic capsule of the final instar larvae of the Anomaloninae and the Metopiinae. Both were observed to have a complete sclerotized epistomal arch, large pointed mandibles (except for the genus *Anomalon*) and lack a hypostomal spur. Townes (1971) has interpreted these similarities as being indicative of a phylogenic affinity between the two subfamilies. However, this resemblance may be due, as Short (1959) and later Viktorov (1968) suggest, to evolutionary convergence resulting from identical modes of life of the larvae, which is the completion of development within the pupae of Lepidoptera. As the hypostomal spur serves as a base for the insertion of the muscles used by the larvae to move the head whilst spinning a cocoon, one might expect that within a group which completes development within the host pupa, and in consequence spins only a thin cocoon, there might be a reduction or even the loss of the hypostomal spur. Similar reduction of the hypostomal spur is found in an unrelated group, the Ichneumoninae, which also complete their development within the host pupa.

In the last comprehensive work dealing with the Ichneumonidae (Townes, 1973) the Anomaloninae are treated as a separate subfamily and placed adjacent to the Metopiinae.

MATERIALS STUDIED AND METHODS USED

In this work every attempt has been made to examine as many specimens as possible from the various genera. A number of species from different zoogeographical regions have been examined so as to avoid biasing the interpretations overmuch in favour of the fauna of any one particular region. The bulk of the material examined is from the collections and accessions of the British Museum (Natural History) (hereafter abbreviated to BMNH); the Hope Department of Entomology, Oxford; the Australian National Insect Collection, Canberra (ANIC); the Queensland Museum (QM); and the author's personal collection. When only a small amount of material was examined mention of this is made in the text.

Three main methods of examination of material have been utilized in this work. Firstly, the genitalia of males and females were examined for characters. Secondly, certain characters, such as relative lengths of wing veins have been quantified, and thirdly, a phenetic investigation of the interrelationship of the various taxa was undertaken.

Preparations of the female genitalia were made by removing the terminal abdominal segments from an insect relaxed overnight in a box dampened with 2 per cent phenol solution. These segments were macerated in 10 per cent potassium hydroxide solution at 100°C and subsequently dehydrated through 30, 50, 70, 90 and 100 per cent ethanols, cleared in xylene and mounted in Canada balsam.

Examination of the male terminalia proved to be somewhat more difficult. Dried material was difficult to interpret due to the complex folding which occurred

in the aedeagal membranes. Whenever possible fresh material or spirit preserved material was used, but this type of material was not available for many tropical specimens examined.

Several methods of reconstituting dried material were tried and comparison of the reconstituted material with fresh material was made. The most successful method for reconstitution was found to be the immersion of the genital capsule in 5 per cent potassium hydroxide solution containing 2 per cent ethanol for 10–15 minutes (depending upon the size of the specimen) at 80°C in a constant temperature water-bath. Preparation of the genitalia, particularly that of small species in non-alcoholic or a more strongly alkaline solution, caused serious distortion of the aedeagal membrane.

The genital capsule was dissected in 30 per cent ethanol containing 2 per cent glycerol and examined initially in glycerol so as to facilitate examination of the structure from all angles.

Drawings were made using high power (×400) and a squared eyepiece. During the course of this work a number of microstructures were observed on the aedeagus. These are referred to as tubercles when rounded convex structures, spines when acute conical structures and spinules when needle-shaped structures.

Morphometric comparisons between genera were based on the measurement of 15 specimens of each sex from the genera considered, except in the case of genera composed of a single or very few rare species. In these cases, measurement was made of all material available and if less than 30 specimens were measured an asterisk is placed against the figures given in the text. Specimens were selected to cover the size range of the genus considered and as many species as were available were examined. The resultant measurements were found to be most conveniently represented as indices (this method has been used for Formicidae by Bolton, 1974). The following indices have been found in some cases to be useful for separating the genera.

BAI Brachio-anal index (forewing)

$$\frac{\text{length of } Cu_1 \text{ between } cua \text{ and } 1m\text{–}cu}{\text{length of } 1A \text{ between } cua \text{ and } Cu_{1b}}$$

BI Brachial index (forewing)

$$\frac{\text{length of shortest distance between } Cu_1 \text{ and } 1A \text{ at extreme distal end of first subdiscal cell}}{\text{length of shortest distance between } Cu_1 \text{ and } 1A \text{ at extreme proximal end of first subdiscal cell}}$$

This quantifies the degree of explanateness of the first subdiscal cell.

CI Cubital index (forewing)

$$\frac{\text{length of } Cu_1 \text{ between } 1m\text{–}cu \text{ and } Cu_{1a}}{\text{length of } Cu_{1b} \text{ between } Cu_{1a} \text{ and } 1A}$$

This quantifies the references of earlier authors to 'nervulus intercepted above, at or below the centre of the brachial cell'.

DAI Dorsal abdominal index

$$\frac{\text{length of dorsum of tergite 2}}{\text{length of dorsum of tergite 3}}$$

DBI Disco-brachial index (forewing)

$$\frac{\text{length of } Cu_1 \text{ between } cua \text{ and } 1m\text{–}cu}{\text{length of } 1m\text{–}cu \text{ between } Cu_1 \text{ and } 2 + 3rm}$$

ICI Intercubital index (forewing)

$$\frac{\text{length of } 2 + 3rm}{\text{length of } M \text{ between } 2 + 3rm \text{ and } 2m\text{–}cu}$$

LAI Lateral abdominal index

$$\frac{\text{length of dorsum of tergite 2}}{\text{apical depth of tergite 2 laterally}}$$

MI Marginal index (forewing)

$$\frac{\text{length of } Rs}{\text{length of } Rs + 2r}$$

NI Nervellar index (hindwing)

$$\frac{\text{length of } Cu_1 \text{ between } cua \text{ and } M}{\text{length of } cua \text{ between } Cu_1 \text{ and } 1A}$$

This quantifies references by earlier authors to 'nervellus intercepted above or below the centre'.

PI Petiolar index

$$\frac{\text{distance from anterior margin of petiolar spiracle to base of tergite 1}}{\text{distance from posterior margin of petiolar spiracle to apex of tergite 1}}$$

RI Radial index (hindwing)

$$\frac{\text{length of } Rs \text{ between } R_1 \text{ and } 1rm}{\text{length of } 1rm \text{ between } Rs \text{ and } M}$$

TI Trochanteral index (hind leg)

$$\frac{\text{length of trochanter measured medio-ventrally}}{\text{length of trochantellus measured medio-ventrally}}$$

Measurements of these lengths were made using an eyepiece micrometer at a magnification of $\times 100$.

In the case of measurement of wing veins error can be introduced by failure to standardize exactly the distance measured. In all cases when the length of a vein between two other veins was measured, the distance recorded was the length of the margin of the vein between the two closest margins of the limiting veins. Thus the breadth of the other veins were not included in the measurement, nor was it necessary to estimate a mid point in the intersection of any two veins.

Classification of the Ichneumonidae is based primarily on comparative studies

of the morphology of the adult insect and, as fossil evidence is scarce, this classification is essentially phenetic. The theoretical aspects of phenetic classification have been discussed at length by Sokal & Sneath (1963; 1973) and a number of their conclusions are particularly relevant to this study. If it is accepted that it is presumptuous to weight any one characteristic in favour of any other positive one, a more accurate interpretation of the suprageneric classification can be made if a large number of characteristics are considered.

From the genera of Anomaloninae under consideration a very large number of characters were considered and those showing little or no intergeneric variation were eliminated. As many of the genera are composed of a few or a single species, the biology of which, because of their rarity, has not been fully investigated, comparison of the immature stages has not been possible on a very large scale.

The characters selected were chosen so as to allow an insect to be scored as either a + or a −. This system of scoring is not meant to infer that a + character is in any way more significant than a − character. In a few cases intermediates have been found and these were scored as ± and were not considered to differ from either a + or a − character. In a very few cases full information was not available; for example, lack of material from either sex prevented the scoring of all genitalia characteristics. In these cases percentage similarities were calculated for the number of scored characters compared and the position of the incompletely scored genera is tentatively shown as dotted lines on the dendrogram.

The characters used, together with their + and − alternatives are listed below and definitions of the characters are included where necessary.

Character	Plus (+)	Minus (−)
00. Lower facial beak-like prominence	present (Text-fig. 165)	absent
01. Medio-clypeal tooth	present	absent
02. Lateral clypeal margin	dentate	without a tooth
03. Eye surface	pubescent	glabrous
04. Lower face centrally	produced	flat
05. Distance between orbit and anterior tentorial pit	less than length of malar space	equal to or more than length of malar space
06. Clypeal sculpture	coriaceous	punctate
07. Inner margins of eyes ventrally	parallel	convergent
08. Occipital carina posterior ocelli	close	distant
(Close is defined as ocelli less than ocellar diameter from occipital carina.)		
09. Interocellar distance	greater than orbital ocellar distance	less than orbital ocellar distance
10. Occipital carina medio-dorsally	complete	interrupted
11. Frons below median ocellus	vertically carinate	without carina
12. Frons between antennae	lamellate	not lamellate
13. Number of labial palp segments	four	three or less
14. Scape apex	almost truncate (Text-fig. 170)	strongly oblique (Text-fig. 172)
15. Length of pedicel	longer than scape	shorter than scape
16. Number of mandibular teeth	one	two
17. Shape of base of cardo	simple (Text-fig. 239)	lobate (Text-fig. 237)
18. Base of mandible	flanged (Text-fig. 164)	simple

Character	Plus (+)	Minus (−)
19. Intersection of genal and hypostomal carina	before mandible base	at mandible base or not joining
20. Head behind eyes	strongly narrowed	parallel or buccate
21. Flagellar segment 10 coloration	rufescent or yellow	black
22. White flagellar band	absent	present
23. Length of antennae	longer than body	not longer than body
24. Accessory carina on occiput	present	absent
25. Pronotum dorsally	long	short

(Long is defined as having median length equal to or longer than the distance from mid line to notaulus base.)

26. Transverse dorsal pronotal crease	present (Text-fig. 208)	absent (Text-fig. 207)
27. Plane of dorsal surface of pronotum	subvertical	horizontal
28. Pronotal tooth	present (Text-fig. 205)	absent
29. Shape of lower margin of pronotum	truncate	acute
30. Notaulus	present and impressed	absent
31. Sternaulus	present and deep	absent or very shallow
32. Anterior mesonotal concavity	present (Text-fig. 208)	absent
33. Mesonotal curvature in profile	abrupt and angular (Text-fig. 206)	gently and evenly (Text-fig. 209)
34. Transverse mesoscutal suture	present (Text-fig. 188)	absent
35. Grooves before scuto-scutellar groove	present (Text-fig. 184)	absent
36. Propodeal shape	globose (Text-fig. 228)	not globose (Text-fig. 226)

(Globose is defined as shape when propodeum, viewed dorsally, is broader than long.)

37. Shape of postscutellum	longer than broad	broader than long
38. Upper end of epicnemial carina	reaching above centre of mesopleuron	below centre of mesopleuron
39. Upper end of epicnemial carina	reaching anterior margin of mesopleuron	not reaching anterior margin of mesopleuron
40. Apical propodeal neck	long	short

(Long is defined as having the propodeal neck longer than the basal width of tergite 1.)

41. Sculpture of propodeal neck	smooth and polished	reticulate or coriaceous
42. Shape of scutellum in profile	more or less flat	very convex
43. Fore coxae ventrally	transcarinate	smooth
44. Fore coxae laterally above trochanter	carinate	without carina
45. Posterior transverse carina of mesosternum	complete	absent or interrupted
46. Length of hind trochanter ventrally	longer than trochantellus	shorter than or equal to trochantellus
47. Shape of hind claw	curved less than 90°	geniculate (100°+)
48. Maximum extent of pecten on hind claw	reaching apex in both sexes	not reaching apex at least in ♂
49. Sexual dimorphism in hind claws	noticeable	not apparent
50. Second hind tarsal segment of ♂	explanate (Text-fig. 177)	not explanate at all
51. Flattened sensory hair on second hind tarsal segment	present	absent

Character	Plus (+)	Minus (−)
52. Number of calcars on mid tibia	one	two
53. Density of spines on fore tibial calcar	scattered (ten or less) (Text-fig. 174)	numerous (Text-fig. 175)
54. Apex of penultimate hind tarsal segment	extended beyond insertion of apical segment	simply truncate
55. Ratio of length of first hind tarsus to second hind tarsus segment in ♂	3·0+	2·5 or less
56. Ratio of length of first fore tarsus to fifth fore tarsus segment in ♂	1·2 or less	1·5+
57. Number of hamuli on R_1	five or less	seven or more
58. Lateral longitudinal carinae of scutellum	complete to apex	incomplete or absent
59. Last abscissa of Cu_1 in hind wing	present at least basally	absent or not discernible basally
60. Radial index	1·2+	1·19−
61. Last abscissa of *Rs* and *M* in forewing	entirely absent	present
62. Distal anterior angle of first subdiscal cell	very acute	obtuse
63. Shape of second discal cell	regularly pentagonal	irregular
64. Cubital index	0·8+	0·7−
65. Disco-brachial index	0·84+	0·83−
66. Brachio-anal index	1·0+	0·99−
67. Brachial index	1·5+	1·49−
68. Position of 2 + 3*rm* in relation to 2*mcu*	distal	opposite or proximal
69. Intercubital index	1·1+	1·0−
70. 2*m–cu*	present	entirely absent
71. Wing tip	infuscate	clear
72. Facial colour of ♂	immaculately yellow	black marked
73. Colour of scutellum compared with mesoscutum	contrasted	concolorous
74. Lateral abdominal index	3·0+	2·9−
75. Dorsal abdominal index	1·4+	1·35−
76. Ratio of distance from petiolar spiracle to posterior margin of tergite to inter spiracular distance	1·5+	1·4−
77. Lateral crease separating epipleuron 3	present	absent
78. Lateral crease separating epipleuron 2	present	absent
79. Length of valvula 3	shorter than tergite 2	longer than tergite 2
80. Shape of apex of valvula 1	abruptly constricted	tapered
81. Postero-dorsal prolongation of valvifer 2	present	absent
82. Curvature of valvula 2	weak	strong
(Weak is defined as having apex inclined at less than 10° to line through base.)		
83. Host preference	lepidopterous larvae	coleopterous larvae
84. Caudal stalk and equatorial disc on ovarian egg	both present (Text-fig. 96)	either or both absent
85. Shape of gonosquamae	extended posteriorly	not extended

Character	Plus (+)	Minus (−)
86. Shape of gonolaciniae	slender and straight (Text-fig. 53)	stout and curved (Text-fig. 52)
87. Ratio of length of proximal apodeme of gonolacinia to median length of basivolsella	0·50+	0·49−
88. Distribution of distivolsellar teeth	central (Text-fig. 65)	peripheral (Text-fig. 77)
89. Gonolacinial teeth	present	absent
90. Shape of ninth abdominal sternite	quadrate	transverse
91. Syntergal fusion	complete	incomplete
92. Spinose ventral aedeagal membrane	present	absent
93. Shape of apex of aedeagus in profile	with dorsal lobe (Text-fig. 108)	without dorsal lobe
94. Continuous apical aedeagal membrane	present	incomplete
95. Shape of base of aedeagal paramere	evenly tapered (Text-fig. 44)	spatulate (Text-fig. 43)
96. Lateral extension of ventral aedeagal membrane	present	absent
97. Apical aedeagal tubercle	present (Text-fig. 133)	absent
98. Constricted extremity of ovipositor	long	short
(Long is defined as having narrowed apex more than 2·0 times as long as median vertical depth of ovipositor.)		
99. Valvula 2 regularly perforated	yes	no

The characters of the genitalia (79–99) are discussed in some detail in the following section.

Insufficient specimens of the genera *Atrometoides*, *Bimentum*, *Brachynervus*, *Porizonopteron*, *Liopterna* and *Calcaneum* were available and therefore these genera have not been included in the numerical investigation.

The type-species of the several genera and subgenera were scored and comparison between each of the species was made. From these comparisons percentage similarities were calculated and the values have been tabulated in the form of a similarity matrix. (The original data have been deposited in the library of the BMNH.) From these results an average linkage dendrogram was produced (Text-fig. 249). Sokal & Michener (1958) used the weighted paired group method (WPGMA) to produce an average linkage dendrogram, but Sokal & Sneath (1973) no longer recommend this method, as when grouping is made a single genus arriving at a synapse is more highly weighted than any one of a group of genera it might join with. To avoid unnecessary weighting, the unweighted pair group method (UPGMA) has been used in this work and therefore

$$S_{(abc),\,d} = 1/3\ (S_{a,\,d} + S_{b,\,d} + S_{c,\,d})$$

where S = similarity and a, b, c and d represent type-species of genera.

THE STRUCTURE OF THE GENITALIA OF THE ANOMALONINAE

Many authors have alluded to the unusual form of the ovipositors of these insects, but the male genitalia have remained neglected since the work of Peck (1937) who commented on the distinctiveness of the two Therionine genera he examined.

The female

In the Ichneumonidae the female genitalia consist of three pairs of gonapophyses, the valvulae. One pair, the first valvulae, articulate with the first valvifers of the eighth abdominal (7th gastral) segment. The other two pairs, the second and third valvulae, articulate with the second valvifers of the ninth abdominal segment. In the living insect the first and second pairs of valvulae are intimately associated and form the ovipositor, whilst the third valvulae, which characteristically articulate terminally on the second valvifers, are compressed and form the ovipositor sheath.

The first valvulae are elongate styliform structures with the distal ends bearing from one to many teeth (Text-figs 8–17). The second valvulae are slightly shorter and mediodorsally, along their entire length, fused. The first valvulae interlock ventrally with the second to form a tube, down which (in most Ichneumonidae) the egg is passed. The third valvulae are transversely striate and externally hirsute (Text-fig. 2). They apparently serve to protect the ovipositor.

Many of the larger (20 mm+) Anomaloninae have the extreme apex of the ovipositor markedly constricted to facilitate oviposition into small first or second instar lepidopterous larvae. There is usually a distinct dorsal subapical notch present (Text-figs 18–20). In the past authors have often placed considerable emphasis on the presence or absence of a subapical ovipositor notch, but in the present subfamily there has been found to be a considerable amount of variation in the shape of the ovipositor. Whilst the majority of genera have a well developed dorsal notch, in *Parania* the apex of the ovipositor is hastate, and strongly laterally compressed, and in *Pseudanomalon*, the ovipositor is apically simply acute (Text-fig. 28). In the majority of genera the ovipositor is rather short, not longer than the length of the dorsum of the second gastral tergite and usually only about as long as the apical abdominal depth. In the genera *Trichomma*, *Philodrymus*, *Podogaster*, in some Nearctic species of *Agrypon*, and in the Anomalonini the ovipositor is longer than the second tergite.

The apices of the first valvulae of the Therionini show a considerable range of variation in shape between the genera. Most genera have the first valvulae slender with the apical 0·1 abruptly constricted, and with the extreme apex bearing between seven and ten minute teeth (Text-figs 10–11). In all Anomaloninae there is a single small irregularly triangular articulated plate, the valvillus (the Hemmplättchen of Oeser, 1961) about 0·15 of the length of the valvula from the valvular apex (Text-fig. 3). These structures have been observed in several other subfamilies of Ichneumonidae by Aubert (1958), Oeser (1961) and Rogers (1972). In living specimens of *Heteropelma calcator* the valvillus projects internally into the egg cavity of the ovipositor. Rogers noted that in *Venturia canescens* the valvillus (=projection) grips the egg in position within the cavity immediately before oviposition.

In the Anomalonini and also in *Parania* the apex of the first valvula is simply acute and the extreme apex bears four or five teeth (Text-figs 8, 12). The valvular apex of *Therion* is elongately acute and bears seven widely spaced teeth (Text-fig. 10), whilst that of *Philodrymus* and *Podogaster* are unusual in being shortly acute with a distinct subapical impression and only a single apical tooth (Text-fig. 16). In *Pseudanomalon gracile* the valvular apex is elongately acute, similar to that of *Therion*, but the valvillus is unusual in being positioned on a large swelling (Text-fig. 14).

The second valvulae are more uniform within the subfamily. The apex is often constricted and the extreme tip is usually weakly decurved. In most genera a distinct subapical notch is present dorsally, but this is noticeably less conspicuous in smaller species. A nodus may occasionally be present and is particularly evident in *Heteropelma* and *Therion* (Text-figs 18, 24). The second valvulae of *Parania*, *Pseudanomalon* and *Ophionellus* are simply acute apically (Text-figs 25, 28, 29) and that of the last genus is perforated by numerous regularly arranged holes throughout its entire length. This is possibly a modification to reduce weight, for in this genus the gaster is exceptionally elongate. The length of the narrowed valvular apex varies considerably from genus to genus, being longest in *Heteropelma* and shortest in some species of *Barylypa* (Text-figs 18, 19).

In *Anomalon*, as in most other Hymenoptera, the third valvulae articulate with the most posterior end of the second valvifers (Text-fig. 4), but in the Therionini the third valvulae articulate subterminally on the second valvifers (Text-figs 5–7) and there is a distinct process, the dorsal apodeme, which extends dorsally and posteriorly to the point of insertion of the valvulae (Text-fig. 2). Although little work has been done on the female genitalia of the Ichneumonidae it would appear that this structure is peculiar to the Therionini. Investigation of other groups thought to be related to the Therionini has revealed that only in some Metopiinae is there a similar process on the second valvifers, and in this subfamily the process when present is small.

Iwata (1958 ; 1960) has examined the structure of the ovaries and the form of the ovarian eggs in the Anomaloninae. The eggs of the genera *Heteropelma*, *Therion*, *Trichomma* and *Habronyx* are remarkable in having a caudal stalk and an equatorial disc, so that the egg is shaped not unlike the traditional Aladdin's lamp (Text-fig. 96). The eggs of other genera are without either an equatorial disc or a caudal stalk, or both. According to Tothill (1922) the function of the equatorial disc is to attach the egg to the inside of the host's integument. Tothill observed that *Therion morio* inserted its ovipositor deep within the young larvae of *Hyphantria* species, and attached an egg on to the body wall of the host opposite the point of insertion of the ovipositor. Askew (1971) states that *Heteropelma* is exceptional in ovipositing, not into the haemocoel but into the gut of lepidopterous larvae. At least in this case the equatorial disc of the egg cannot be used in the same way as Tothill suggested.

The male

The male genitalia are considerably more complex than those of the female. The homology of the genitalia of male Hymenoptera with that of other insect

orders is not resolved. It is not within the scope of the present work to discuss the possible homologies of the Ichneumonid male genitalia, and previous authors (Peck, 1937; Snodgrass, 1941) have discussed this matter at length. In the present work the terminology follows that of Peck, but this is not intended to imply that his interpretation of the genital structure is the more correct. Peck specifically investigated the genitalia of the Ichneumonidae, and it is therefore more convenient to utilize his terminology.

The male genitalia consist of a capsule formed by a pair of lateral gonosquamae, proximally surrounded by an annular gonocardo which is formed by the fusion of a pair of lateral semicircular sclerites. The gonosquamae enclose a pair of clasping organs, the volsellae (Text-figs 30–33). In the majority of Ichneumonidae the volsellae are sclerotized and only joined to the gonosquamae by a membrane. The volsellae are subdivided into two regions, the basivolsella and distivolsella. The former is a flattened region with a longitudinal, heavily sclerotized bar, the basivolsellar strut, which separates the basivolsella into two areas, the ventral and dorsal areas (Text-fig. 31). Partially fused to the distal margin of the ventral area is a hollow finger-like structure, the distivolsella. The distivolsella bears spines on its inner or clasping surface.

Associated with the distivolsella is the gonolacinia which in most Ichneumonidae is not fused with the volsella, although in some species of *Cremastus* Gravenhorst (Cremastinae) it is proximally fused to the ventral area of the basivolsella. The distivolsella and gonolacinia together effect clasping.

In the centre of the genital capsule is the intromittant organ, the aedeagus. The shape of the typical Ichneumonid aedeagus is a weakly depressed cylinder having its distal ends lengthened into a pair of rod-like projections, the parameres.

Included in this discussion of the male genitalia are the sclerites that are associated with the genital capsule. The genital capsule is supported anteriorly by the syntergum and the ninth abdominal sternite. The syntergum is usually an inverted U-shaped sclerite formed by the fusion of the ninth and tenth abdominal tergites. The posterior margin of the syntergum bears a pair of appendages, the pygostyles, which are probably homologous with the cerci of other insect orders. In some Ichneumonidae there is a dorsal longitudinal membranous area which divides the syntergum into a pair of syntergites. The ninth abdominal sternite is a concave almost quadrate sclerite laterally joined by membranes to the lower lateral corners of the syntergum.

Little use has previously been made of characters of the male genitalia of the Ichneumonidae. Some workers have found that it is possible to separate species within a genus (Townes, 1938; Pratt, 1939; Perkins, 1960) but other workers have found that the structure of the genitalia is not very useful for the separation of genera (Peck, 1937). Examination of the genitalia of the Anomaloninae has shown that it is usually possible to place a species in the most appropriate genus by examination of the male genitalia.

In the Anomaloninae there is generally a single syntergum present, but in some genera the syntergites are separated by a narrow mediodorsal longitudinal membranous area. The mid dorsal fusion of the syntergites is not apparently dependant

upon the size of the insect as in *Habronyx* (*Habronyx*) species (length about 30 mm) and *Perisphincter* species (length about 10 mm) separate syntergites are present, whereas in *Heteropelma* species (length about 25 mm) and *Clatha* species (length about 7 mm) a single syntergum is present. Peck (1937) noted that *Therion circumflexum* had separate syntergites, but of the dozen or so specimens of this species examined during the preparation of this work, all were found to have a syntergum, with at the most a small V-shaped notch in the dorsal anterior margin. It is possible, therefore, that at least in some species there is intraspecific variation in the degree of fusion of the syntergites.

There was found to be a considerable degree of variation in the shape of the syntergum laterally, but this variation in shape was not found to be useful taxonomically. *Ophionellus* species, however, are exceptional in having the pygostyles inserted very much closer to the median dorsal line of the tergite than in other genera (Text-fig. 94).

The ninth abdominal sternites of the Anomaloninae were found to be rather evenly sclerotized (except in *Clypeocampulum*) rectangular transverse plates with slender median anterior apodemes. The posterior margin varies in shape from truncate to fully semicircularly rounded (Text-figs 38–42). There was found to be some degree of variation of the shape of these sclerites, even within a species, and thus their shape is of little taxonomic use. A similar variation in the shape of these sclerites has been noted for another Ichneumonid group, Phygadeuonini (Horstmann, 1967). The ninth abdominal sternite of *Pseudanomalon* was found to be exceptional in being very transverse, more than three times as broad as long, whereas in most genera this sclerite is about twice as broad as long. The ninth abdominal sternite of *Trichomma* is unusual in being quadrate with a median indentation in the posterior margin (Text-fig. 41). The general form of this sclerite amongst the Anomaloninae was found to be similar to those of the Ophioninae, and rather different from those of the Metopiinae which were found to have an anterior lobule in place of a median apodeme.

There is considerable intraspecific and intrageneric variation in the shape of the gonosquamae. Similar variation in the shape of these sclerites has been observed in another Ichneumonid group, the Hemitelini (Blunck & Kerrich, 1956). Generally the gonosquamae were found to be quite truncate (Text-fig. 33), but in one genus, *Ophionellus*, they were consistantly observed to be very elongate (Text-fig. 93).

The gonolaciniae are strongly curved in most genera and bear a number of small teeth along their distal apical margin. The majority of genera have the gonolaciniae of the form shown in Text-figs 59–63, although a few genera have distinctly shaped gonolaciniae. Those of *Anomalon* and *Neogreenia* are evenly curved, weakly pointed and with a narrow proximal apodeme (Text-fig. 50). The gonolaciniar apodeme varies considerably in length between the genera. In *Heteropelma* the apodeme is long, only weakly angled from the axis of the gonolacinia, whereas in *Therion* it is short and strongly angled from the gonolaciniar axis (Text-figs 52, 57). The gonolaciniae of *Anomalon biguttatum* are remarkable in being moderately elongate and weakly curved (Text-fig. 51). *Clatha* and *Atrometus* are exceptional in having the gonolaciniae very elongate, slender, almost straight, centrally

swollen and bearing large spines (Text-figs 34, 53). The general form of the Anomalonine gonolacinia is similar to that of the Ophioninae, which although more acute terminally (Text-fig. 37) bear a number of spines on the distal apical margin. Both differ markedly from the Metopiinae where the gonolacinae bear lateral tubercles and often have a distinct fenestra (Text-fig. 35).

A comparison of the claspers of the three subfamilies Anomaloninae, Ophioninae, and Metopiinae has shown that whereas the modes of action of those of the former two subfamilies are fundamentally similar, that of the latter differs markedly. In the Anomaloninae and Ophioninae, the clasping face of the distivolsella is somewhat ridged and this ridge bears spines. Clasping is effected between this ridge and the distal apical teeth of the gonolacinia (Text-figs 31, 32). In the Metopiinae the clasping face of the distivolsella is planar and bears a large number of well developed conical teeth. The gonolacinia has the distal edge obliquely truncate with a large number of minute tubercles arranged laterally. Clasping is effected between the distivolsellar teeth and the apico-lateral corner of the gonolacinia (Text-figs 35, 36).

The volsellae of the Anomaloninae are completely sclerotized (Text-figs 30–33). The dorsal area is more or less absent and the dorsal margin of the volsella is formed by the basivolsellar strut. This strut has a small basal apodeme and is distally planar at the articulation with the gonolacinia. The distivolsella is intimately fused to the ventral area of the basivolsella.

The clasping face of the distivolsella varies considerably and the form of this face is a useful taxonomic feature. *Trichomma*, *Atrometus* and *Clatha* are exceptional in having this face centrally swollen and bearing many elongate spines on the proximal side of the swelling (Text-figs 34, 65, 71). *Anomalon* differs from the other genera in having the clasping face weakly distally swollen and bearing spines over the rather extensive proximal slope (Text-fig. 67). All other genera examined were found to have a ridge extending more or less diagonally across the face of the distivolsella. The extent to which this ridge is developed varies from genus to genus. It is most developed in the genera *Therion*, *Heteropelma* and *Habronyx* and least well developed in the genera *Pseudanomalon*, *Barylypa* and *Philodrymus* (Text-figs 64–83).

The position of the spines is a useful diagnostic feature of certain genera. Both *Therion* and *Heteropelma* usually have the most proximal spines paired (Text-figs 69, 70). *Aphanistes* is distinct in having large regularly arranged conical spines (Text-fig. 73), whereas *Tanypelma* has the spines distributed on the ventral portion of the distivolsella (Text-fig. 75) and *Pseudanomalon* has a very few spines on the apico-ventral margin (Text-fig. 77).

The shape of the entire distivolsella is a useful feature of certain genera. *Aphanistes* has the distivolsella centrally a little angled and distally truncate, whilst *Vernamalon* has the distivolsella markedly acute apically. The distivolsellae of the genera *Parania* and *Gravenhorstia* are rather quadrate (Text-figs 74, 80) and differ from the other genera examined in having the distivolsella more than 0·8 times as broad basally as long.

In all Anomalonine genera examined the distivolsellar apodeme was found to be

large and simple, like those of the Ophioninae, and quite unlike the bipartite apodeme found in some of the Metopiinae (Text-fig. 35).

All the Anomalonine genera examined were found to bear a number of obvious microtrichia along the margin of the volsella remote from the gonolacinia. It is suggested that these microtrichia are mechanoreceptors.

Of the parts of the male genitalia, the aedeagus is undoubtedly of the most interest to taxonomists. It is for many Anomalonine genera singularly characteristic in form. It may prove possible to separate males of hitherto much confused species by examination of the structure of this organ. Sĕdivy (1956) used a difference in the form of the aedeagus to distinguish between *Therion circumflexum* and *T. giganteum*.

The aedeagi of the Anomaloninae are much less elongate than the corresponding organs of either the Metopiinae or the Ophioninae although the aedeagus of *Ophionellus* superficially resembles those of the latter subfamily.

The aedeagus of *Anomalon* is terminally evenly rounded and possesses a sclerotized region which is produced into a proximally directed spine (Text-fig. 86) that is quite unlike any structure in the aedeagus of the other genera examined.

The Therionini exhibit a wide variety of form in the aedeagus. Generally the aedeagi are somewhat terminally lobate and characteristically with one or more membranous areas present. In the genera *Barylypa*, *Aphanistes*, *Habronyx* (*Habronyx*) and to a lesser extent *Heteropelma* and *Gravenhorstia*, the ventral membranous region is covered with minute spines (Text-figs 100–105). In other genera this region is smooth (Text-figs 132–139).

Trichomma is particularly unusual in having an extensively membranous aedeagus, which is noticeably reticulately sculptured and has a spinose area medio-apically (Text-figs 130, 131).

The shape of the extreme base of the parameres varies considerably within the Therionini. The majority of genera have the paramere base either acute or bluntly rounded (Text-figs 44, 47). In some genera the base is flattened and spatuliformly explanate (Text-figs 45, 46). This development is most extreme in the genus *Spolas* (Text-fig. 46). In *Vernamalon* the paramere base is flattened and shaped like a spearhead (Text-fig. 48) whilst among *Parania* species the base is hastate (Text-fig. 45). *Philodrymus* and *Podogaster* are distinctive in having the bases of the parameres markedly angled and bearing a large apodeme (Text-fig. 49).

A more detailed discussion of the variations of the form of the aedeagus both within and between genera is included in the following sections.

EVALUATION OF CHARACTERS OF THE GENERA OF THE ANOMALONINAE

The generic classification in this work broadly follows that of Townes (1971) who, in his notable series of monographs, brought together, redescribed and compared the Ichneumonid genera of the world, thus making further research into the relationships within any one group considerably easier.

As a result of investigation of genitalia and morphometric evaluation of certain features, some changes have been made in the system of classification. Certain

genera have been broadened to include exceptional species, and some unplaced species have been placed in newly erected genera. In every case the author has avoided erecting new and possibly spurious genera for every atypical species examined. Only when a species or group of species has been found to differ in a considerable number of characters from those of any described genus, a new genus has been erected.

Throughout this work emphasis is placed on the investigation of large numbers of characters. This is because the Ichneumonidae in particular show a large number of combinations of variations of a fairly small number of features. In the past emphasis has often been placed on a single feature (for example the presence or absence of notauli) and the placing of species in a genus depended almost wholly on this feature. This single character may well be reliable for the fauna of a particular zoogeographic region, although in another region this same character may break down. Consequently, a species similar to the type-species of a certain genus and differing perhaps only in the so called 'diagnostic feature' of this genus, may easily be placed in a separate genus. This is particularly true if the 'diagnostic feature' is very apparent. For example, *Erigorgus* and *Gravenhorstia* are very similar genera but *Gravenhorstia* is unusual in having a compact gaster, and is thus easily recognizable. Because of this obvious difference, the two genera have been treated as being quite distinct even though more recent evidence is constantly revealing that there are intermediate species. A number of the 'diagnostic characters' which in past works have received considerable emphasis are discussed below.

The position of vein Cu_{1a} in the forewing has been considered an important feature. As early as 1849, Wesmael divided 'Anomalon' (that is the group containing the majority of Therionine species, and excluding only *Therion*, *Heteropelma* and *Trichomma*) into those having Cu_{1a} closer to 1*m–cu* than to 1*A*, and those having Cu_{1a} closer to 1*A* than to 1*m–cu*. All authors since then have used this feature to facilitate generic separation. In the present work the position of this vein has been defined by the cubital index, CI. Chart 1 shows the ranges of CI for the larger genera. From this it can be seen that some genera consistently have CI greater than 1·00 (that is Cu_{1a} closer to 1*A*; e.g. *Aphanistes*) and other genera consistently have CI less than 1·00 (that is Cu_{1a} closer to 1*m–cu*; e.g. *Barylypa*). A few genera and subgenera have been found to be intermediate, having a value of CI distributed about 1·00. One of these, *Habronyx* (*Camposcopus*) was previously classed as having CI greater than 1·00, but it can clearly be seen that a number of specimens have CI less than 1·00. As this character is invariably found in keys after the separation of only the genera *Therion*, *Heteropelma* and *Trichomma*, there is a considerable chance that an inexperienced worker, failing to recognize the species immediately, would run the specimen down the wrong side of the key and place it within *Agrypon*.

Chart 2 shows the values of the discobrachial index DBI. This quantifies the position of the intersection of Cu_1 and 1*m–cu* with relation to the central axis of the discosubmarginal cell. In most works, the genera *Therion* and *Heteropelma* have been separated from the remaining genera by describing them as having Cu_1/1*m–cu* at the centre of the discosubmarginal cell (i.e. DBI = 1·00) whilst

other genera were described as having Cu_1/*1m-cu* before the centre of the disco-submarginal cell (i.e. DBI less than 1·00). It can be seen that there is a definite range of overlap between *Habronyx* (*Habronyx*) and *Heteropelma*.

The presence of a transverse flexible suture immediately in front of the scuto-scutellar groove is a feature found only in the Ichneumonidae amongst a few Therionine genera (Podogastrini of Townes, 1971), and incompletely in the Xoridinae. This suture has also been found to be present in some species referable to genera which are placed in the Gravenhorstiini of Townes. As the presence or absence of this suture is the only proposed consistent difference between these two tribes, the occurrence of the suture in both groups makes the division into two separate tribes untenable.

In *Philodrymus*, *Ophionellus*, *Podogaster* and *Clatha* there is a broad shallow scuto-scutellar groove, which is continuous laterally with the axillae (Text-figs 188–191) and may represent a dorsal axillary bridge, a feature which has been observed in some Chalcidoidea (Grandi, 1920). A median longitudinal section through the thorax has shown that there is a discontinuity in the sclerotized exocuticle, and internally the margins of this discontinuity are rounded and separate (Text-fig. 191).

In *Ophiopterus* two secondary grooves are present immediately anterior to the suture. These grooves are impressed in the exocuticle and are not areas of exocuticular invagination (Text-figs 184, 185). In this genus the scuto-scutellar groove is deeper and narrower than in those of the aforementioned genera. The scuto-scutellar morphology of *Ophiopterus* is similar to that of *Phaenolabrorychus*. In the latter genus, however, three transverse grooves only are present, the most posterior of these being in a similar position to the suture in *Ophiopterus*. In section, the posterior groove was found to be the deepest, but did not penetrate the exocuticle, and was observed to be continuous with the lateral scuto-axillary invagination (Text-figs 180, 181). Cuticular wedges of the type described by Sharplin (1963) found internally in areas where flexibility is required, have not been found to be present in the scuto-scutellar region of these insects.

In *Vernamalon* the scuto-scutellar groove is deep and the posterior part of the scutum is almost touching the anterior margin of the scutellum. A transverse suture is present, but it is infolded so that in section it is horizontal to the longitudinal axis of the insect (Text-figs 186, 187). Dorsally the suture is obscured by an overhanging margin of the scutum. In many insects it is difficult to see, except by dissection, whether or not a similarly placed suture is present. This is the case with many species at present placed within *Agrypon*. In some specimens in the BMNH collections (labelled *Trichionotus arquatum* (Gravenhorst)) and in an undescribed species of *Agrypon*, a continuous suture is present. These specimens otherwise resemble the majority of other species of *Agrypon* in having the fore coxae carinate. In *A. albiditarsum* a suture is also present, although it is interrupted laterally by a short area of fusion between the scutum and the axillae (Text-fig. 182). In the major ty of species in this genus there has not been found to be any trace of a suture present, except at the extreme lateral margins of the scutum (Text-fig. 178).

Discussion of some remaining characters is included where relevant in the generic diagnoses.

Keys to Genera and Subgenera

The adult Anomaloninae

1 Epipleuron of tergite 3 separated by a longitudinal crease below the spiracle; mid tibia with a single spur; 2 + 3*rm* distal to 2*m–cu* or absent; posterior ocellus closer to anterior ocellus than to an often incomplete occipital carina; ♀ with valvula 3 longer than tergite 2; ♂ with gonolacinia weakly curved, without teeth (Text-fig. 50); parasites of coleopterous larvae . . . 2

– Epipleuron of tergite 3 not separated by a longitudinal crease (Text-fig. 226); mid tibia with 2, or rarely with a single apical spur; 2 + 3*rm* usually proximal to, rarely opposite or distal to 2*m–cu*; posterior ocellus usually closer to occipital carina than to anterior ocellus (Text-fig. 175); ♀ often with valvula 3 shorter than length of tergite 2; ♂ with gonolacinia moderately to strongly curved, usually with obvious apical teeth present; parasites of lepidopterous larvae 3

2 (1) Length of 2 + 3*rm* approximately equal to that of abscissa of *M* between 2 + 3*rm* and 2*m–cu*; hindwing with abscissa of *Rs* between R_1 and 1*m–cu* greater than 0·9 times as long as 1*m–cu*; flagellum of ♀ never with a white band. (Cosmopolitan) . . . . . ***ANOMALON*** Panzer (p. 85)

– Length of 2 + 3*rm* less than 0·3 times as long as abscissa of *M* between 2 + 3*rm* and 2*m–cu*; hindwing with abscissa of *Rs* between R_1 and 1*m–cu* less than 0·5 times as long as 1*m–cu*; flagellum of ♀ often with a white band. (Neotropical and southern Nearctic) . . . ***NEOGREENIA*** Viereck (p. 88)

3 (1) Mid tibia with two distinct apical spurs 4

– Mid tibia with a single apical spur 41

4 (3) Forewing with 2 + 3*rm* angled near base and distal to 2*m–cu* (Text-fig. 197); scape strongly oblique apically, especially in the ♀ (Text-fig. 172) so that shorter side is less than 0·5 times as long as longer side.

Apex of clypeus with a pair of median apical teeth; flagellum of ♀ usually with a white band. (Neotropical and southern Nearctic) ***OPHIOPTERUS*** Brullé (p. 84)

– Forewing with 2 + 3*rm* straight; scape apically truncate or weakly oblique but always with shorter side more than 0·5 times as long as longer side . . 5

5 (4) Hindwing with distal abscissa of Cu_1 present, at least proximally, rarely with this vein weakly pigmented 6

– Hindwing without any trace of distal abscissa of Cu_1; Cu_1 + *cua* evenly curved or straight, without basal stub of distal abscissa of Cu_1 26

6 (5) Forewing with Cu_1 between *cua* and 1*m–cu* 0·8 or more (usually 0·86 or more) times as long as 1*m–cu* (Text-fig. 196); lower anterior margin of pronotum usually with a distinct tooth (Text-fig. 205); clypeus without a median apical tooth 7

– Forewing usually with Cu_1 between *cua* and 1*m–cu* 0·75 or less times as long as 1*m–cu* (Text-fig. 1); rarely, if more than 0·75, then clypeus with a median apical tooth and lower anterior margin of pronotum without a tooth . . 9

7 (6) Posterior transverse carina of mesosternum interrupted before each mid coxa; lower face at narrowest point at least 0·85 times as broad as height of lower face from medio-clypeal apex to antennal base; hind tarsal claws simply curved.

Lower face often yellow with black vertical stripes; ♂ with hind tarsi

ventrally flattened, glabrous, often with a longitudinal carina. (All regions except Australian) . . . . . ***THERION*** Curtis (p. 49)

– Posterior transverse carina of mesosternum complete; lower face at narrowest point at most as broad as height of lower face from medio-clypeal apex to antennal bases; hind tarsal claws apically turned through more than 90° (except in one Australian species) (Text-fig. 221) 8

8 (7) Scutellum in profile very convex; nervellar index more than 0·80; second hind tarsal segment of ♂ without a flattened impressed area. (Nearctic) ***TANYPELMA*** Townes (p. 52)

– Scutellum in profile flattened; nervellar index less than 0·60; second hind tarsal segment of ♂ with a flattened impressed area bearing broad hairs (Text-fig. 177) (except in *H. elongatum*). (Palaearctic and Indo-Australian regions) . . . . . ***HETEROPELMA*** Wesmael (p. 51)

9 (6) Apex of clypeus concave or truncate, without a median apical tooth (Text-fig. 159); mesoscutum in profile smoothly and evenly rounded, notauli absent. (Palaearctic and Mediterranean) 10

– Apex of clypeus convex or pointed, usually with a median apical tooth, if rarely this tooth is absent then either mesoscutum in profile is abruptly rounded, or notauli are present, if very rarely clypeus is truncate or weakly concave then median apical tooth is distinct (Text-figs 160–163) . . 11

10 (9) Epipleuron of second gastral segment not separated by a crease; tergite 2 laterally only slightly longer than deep apically; occipital carina complete; forewing with 2 + 3*rm* opposite or slightly proximal to 2*m-cu*.
Large yellow and black insects. (North Africa) ***AUBERTIANA*** Viktorov (p. 61)

– Epipleuron of second gastral tergite separated by a crease; tergite 2 laterally more than 2·0 times as long as deep apically; occipital carina absent dorsally; forewing with 2 + 3*rm* distal to 2*m-cu*.
Medium sized, reddish brown and black insects. (Turkey and southern U.S.S.R.) . . . . . ***ATROMETOIDES*** Fahringer (p. 62)

11 (9) Eyes with dense elongate pubescence; lower face at narrowest point less than 0·55 times as broad as distance from medio-clypeal apex to antennal base (Text-fig. 158); hind wing with radial index less than 1·20; ♀ with valvula 3 as long as tergite 2; ♂ with distivolsella with central hump bearing elongate spines (Text-fig. 65).
Often parasitic on fruit-mining or other concealed lepidopterous larvae. (Cosmopolitan) . . . . . ***TRICHOMMA*** Wesmael (in part) (p. 63)

– Eyes at most shortly and sparsely pubescent; lower face at narrowest point more than 0·65 times as broad as distance from medio-clypeal apex to antennal base; hind wing with radial index often more than 1·35; ♀ with valvula 3 less than 0·65 times as long as tergite 2 (except in some Nearctic species); ♂ with distivolsella with short spines arranged diagonally, transversely or peripherally 12

12 (11) Basal segments of the gaster elongate; tergite 2 more than 1·45 times as long as tergite 3, and more than 2·8 times as long as deep apically (when measured laterally); tergite 3 laterally, longer than deep 13

– Basal segments of gaster not elongate; tergite 2 less than 1·35 times as long as tergite 3, and 2·5 times as long as deep apically (when measured laterally); tergite 3 laterally, almost quadrate (Text-fig. 226) 23

13 (12) Fore coxae, when viewed ventrally, with a carina discernible along their anterior edge.
Forewing with cubital index less than 0·6. (Cosmopolitan) ***AGRYPON*** Foerster (in part) (p. 66)

– Fore coxae, when viewed ventrally, smooth without a trace of carina along anterior edge 14

14 (13) Posterior transcarina of the mesosternum complete; forewing with 2 + 3*rm* distal to 2*m–cu*.

Ocelli large, posterior ones separated from occipital carina by less than 0·3 times their diameter; hind tarsal claws pectinate to apices. (Old World tropics) . . . . . ***PSEUDANOMALON*** Szépligeti (p. 48)

– Posterior transverse carina of the mesosternum interrupted in front of each mid coxa, or vestigial; forewing usually with 2 + 3*rm* proximal to 2*m–cu*, rarely opposite or distal 15

15 (14) Pronotum dorsally flat, without any trace of a transverse groove, or if rarely with a very indistinct groove, then occipital carina absent centrally or laterally; forewing with cubital index less than 0·65, generally less than 0·45 . 16

– Pronotum dorsally with a distinct transverse groove, in a few Australian species with the groove weakly impressed, but then always with the occipital carina complete; forewing with cubital index greater than, 0·75, usually greater than 0·95 17

16 (15) Occipital carina usually entirely absent on upper 0·5 of head, laterally strongly raised, rarely with central part of occipital carina present and upper lateral part absent; aedeagus with raised vertical keels immediately before the apex (Text-fig. 85); epomia usually strongly divergent from anterior margin of pronotum. (Central American and Nearctic) . ***CORSONCUS*** Townes (p. 46)

– Occipital carina complete; aedeagus without keels, heavily and rather evenly sclerotized; epomia weakly divergent from anterior margin of pronotum. (Cosmopolitan) . . . . . ***BARYLYPA*** Foerster (p. 44)

17 (15) First segment of hind tarsus prolonged on its upper side beyond the insertion of the second segment; mandible often with a single tooth. (North Africa and U.S.S.R.) . . . . . ***PORIZONOPTERON*** Shestakov (p. 63)

– First segment of hind tarsus not prolonged on upper side beyond the insertion of the second segment; mandible with two teeth except in a few Australian and Neotropical species 18

18 (17) Lower anterior corner of pronotum produced into a small rather weakly sclerotized tooth (Text-fig. 201); postscutellum much longer than broad (Text-fig. 230); propodeum when viewed dorsally more than 2·5 times as long as broad centrally, anteriorly parallel sided.

Hind trochanter and trochantellus subequal in length; scutellum usually yellow. (Western Palaearctic)

HABRONYX subgenus ***HABROCAMPULUM*** subgen. n. (p. 38)

– Lower anterior corner of pronotum without a tooth; postscutellum broader than long (in a few Australian species quadrate); propodeum less than 2·0 times as long as broad centrally 19

19 (18) Mesoscutum in profile with an angular concavity just before anterior margin, so that extreme front margin is horizontal (Text-fig. 208); tarsal claws pectinate to apices (Text-fig. 212); frons usually with a median vertical lamella.

Ocelli often very large, posterior ones separated from occipital carina by less than 0·3 times their diameter. (Cosmopolitan)

APHANISTES Foerster (p. 41)

– Mesoscutum in profile without a concavity before anterior margin, or rarely in a few Australian species, when weak anterior concavity is present, then tarsal claws are not pectinate to apices and the frons is without a median vertical lamella 20

20 (19) Mesoscutum in profile anteriorly evenly rounded (Text-fig. 209); notauli entirely absent, not even represented by an area of coarser sculpture.

Lower corner of pronotum simply acute (Text-fig. 204); claws of ♂ long, weakly curved, pectinate only at extreme base (Text-figs 215–218), those of ♀

shorter, moderately curved, pectinate to, or just beyond, the centre; ♂ with apex of aedeagus with a dorsal lobe. (Cosmopolitan)

GRAVENHORSTIA subgenus ***ERIGORGUS*** Foerster (p. 60)

– Mesoscutum in profile weakly to strongly abruptly rounded (Text-fig. 206); notauli present, strongly impressed, rarely quite weakly impressed but then discernible by being strongly rugose 21

21 (20) Forewing with marginal index greater than 1·50, usually more than 1·80; epicnemial carina extending above centre of mesopleuron, its upper end reaching the anterior margin of the pleuron; hindwing with nervellar index greater than 3·5.

Tarsal claws short, not reaching beyond apex of arolium, pectinate except apically; small species (1·5 mm or less). (Holarctic)

HABRONYX subgenus ***CAMPOSCOPUS*** Foerster (p. 37)

– Forewing with marginal index less than 1·50, usually less than 1·40; epicnemial carina usually not extending above the centre of the mesopleuron except in a few large (3·0 mm +) species; hindwing with nervellar index less than 2·5, usually very much less 22

22 (21) Trochanter more than 1·5, usually more than 1·6 times as long as trochantellus when viewed ventrally; clypeus invariably with median apical tooth; ♂ with aedeagus with a well developed dorsal membranous area that resembles a crest in dried specimens; distivolsella slender, apically swollen; large to very large insects (3·0 mm +); sometimes with the tarsal claws pectinate nearly to apices. (Cosmopolitan)

HABRONYX subgenus ***HABRONYX*** Foerster (p. 36)

– Trochanter at the most 1·45, usually less than 1·4 times as long as trochantellus when viewed ventrally; clypeus varying from medially pointed with a small apical tooth to simply convex, without a tooth; ♂ with aedeagus with a poorly developed dorsal membranous area that does not appear crest-like in dried specimens; distivolsella moderately broad, not at all swollen at apex; moderate sized insects (1·5–2·0 mm); tarsal claws sexually dimorphic, those of ♂ long, weakly curved and pectinate at extreme base, those of ♀ shorter, more strongly curved and pectinate to centre (Text-figs 213, 214). (Australian)

HABRONYX subgenus ***AUSTRANOMALON*** subgen. n. (p. 39)

23 (12) Hind tarsal claws with a median 90° bend; vertex with posterior ocelli separated from the occipital carina by at least twice their diameter; occipital carina often centrally interrupted; abdomen weakly depressed.

Large, pale to dark coloured insects; wings often with dark patterning. (Southern Africa) . . . . . ***ENCARDIA*** Tosquinet (p. 53)

– Hind tarsal claws medianly curved, not at all geniculate (Text-fig. 211); vertex with posterior ocelli separated from the occipital carina by less than 1·5 times their diameter; occipital carina complete 24

24 (23) Tergite 2 laterally about 1·6 times as long as deep apically, its epipleuron wide and conspicuous; lower face with a large median tubercle immediately below the antennae; lower tooth of mandible almost equal in length to the upper.

Large black and yellow insects. (Mediterranean)

GRAVENHORSTIA subgenus ***GRAVENHORSTIA*** Boie (p. 58)

– Tergite 2 laterally at least 2·0 times as long as deep apically, its epipleuron narrow; lower face planar, with at the most a minute median tubercle below base of antennae; lower mandibular tooth distinctly the shorter . . 25

25 (24) Mandible with a large ventrobasal lobe (Text-fig. 164); eyes glabrous; tarsal claws pectinate for most of their length; apex of clypeus angular with an obtuse point (Text-fig. 157); face coarsely punctate.

Abdomen immaculately red. (Spain)

GRAVENHORSTIA subgenus ***RIBASIA*** Ceballos (p. 61)

– Mandible without a large basal lobe; tarsal claws at most pectinate only basally; apex of clypeus margined, with a very small median tooth; face finely punctate.
Yellow and black banded insects. (Mediterranean and central Asia)
GRAVENHORSTIA subgenus ***KOKUJEWIELLA*** Shestakov (p. 59)

26 (5) Fore coxae, when viewed ventrally, with a carina discernible along their anterior edge, rarely with carina very weak (Text-fig. 224) 27

– Fore coxae, when viewed ventrally, smooth without a trace of a carina along anterior edge (intermediate specimens will key through either couplet) . 29

27 (26) Pedicel as long as, or longer than, scape (Text-fig. 171); mesoscutum with transverse furrows before scuto-scutellar groove (Text-fig. 180); posterior apex of propodeum produced into an elongate unsculptured 'neck'.
Apex of clypeus with a pair of small teeth. (Neotropical)
PHAENOLABRORYCHUS Viereck (p. 69)

– Pedicel at most 0·8 times the length of scape, generally less than 0·6 times; mesoscutum without transverse furrows, at most with indistinct wrinkling before scuto-scutellar groove; posterior apex of propodeum either not produced into an elongate neck, or rarely, if produced into a neck, then the neck is coarsely reticulately sculptured 28

28 (27) Carina on fore coxae almost entirely encircling the coxa, present on outer side above the trochanteral socket as well as on anterior and inner sides; clypeal apex with a small median and two minute lateral teeth, the lateral teeth sometimes indistinct, rarely with all teeth indistinct, the clypeus therefore appearing simply convex apically. (Indo-Papuan and Australian regions)
PERISPHINCTER Townes (p. 68)

– Carina on fore coxae on anterior and often inner sides, never on outer side above the trochanteral socket (Text-fig. 224); apex of clypeus usually with a strong median tooth, rarely convex with a small median tooth. (Cosmopolitan)
AGRYPON Foerster (p. 66)

29 (26) Mesoscutum with a transverse suture anterior to the scuto-scutellar groove; posterior transverse carina of mesosternum complete 30

– Mesoscutum without a transverse suture; posterior transverse carina of mesosternum complete or interrupted before mid coxae 36

30 (29) Forewing with *1m–cu* and Cu_{1a} basally separated by a distance at least 0·25 times the length of Cu_{1b}.
Apex of propodeum extended into a long neck, the neck not sculptured (Text-fig. 227); forewing often with distal margins clouded. (Ethiopian region) . . . . . ***CECHENODES*** Townes (p. 76)

– Forewing with Cu_{1a} and *1m–cu* basally united, or separated by at most a distance equal to less than 0·1 times the length of Cu_{1b} 31

31 (30) Sternaulus present as a foveolate impression that extends 0·3–0·6 times the length of mesopleuron; lower distal corner of first subdiscal cell separated from a very weakly impressed vannal notch by a distance equal to about 0·9 times length of *cua*, and with a pigmented region resembling a vein that extends from lower distal corner of first subdiscal cell to hind margin of wing (Text-fig. 195); hindwing with 3–5 hamuli on R_1 32

– Sternaulus absent or indistinct, not strongly impressed; lower distal corner of first subdiscal cell close to vannal notch, never separated by more than 0·5 times length of *cua*, and if rarely with a pigmented region resembling a vein present, then this is parallel to posterior margin of wing (Text-fig. 192); hindwing usually with 6 or more hamuli on vein R_1 33

32 (31) Apex of propodeum extended into a neck that reaches to or beyond apex of hind coxa; inner margins of eyes very strongly convergent ventrally, at their closest point separated by a distance about equal to width of base of man-

dible; hindwing with radial index less than 1·2; petiolar spiracles very close to hind margin of tergite. (Neotropical region) ***PODOGASTER*** Brullé (p. 80)

– Apex of propodeum not extended into a neck, not reaching beyond centre of hind coxa; inner margins of eyes moderately convergent ventrally, at their closest point separated by a distance equal to at least twice the width of the mandible base; hindwing with radial index more than 1·5; petiolar spiracles not unusually close to posterior margin of tergite. (Neotropical region) ***PHILODRYMUS*** Townes (p. 81)

33 (31) Occipital carina separated from posterior ocelli by more than 3·0 times the diameter of an ocellus; clypeus with a pair of apical teeth (Text-fig. 233).

Notauli represented by coriaceous areas which in posterior half of mesoscutum are produced into a raised ridge. (Ethiopian region) ***VERNAMALON*** gen. n. (p. 77)

– Occipital carina at most separated from posterior ocelli by a distance equal to 1·5 times the diameter of an ocellus; clypeus with a single median tooth . 34

34 (33) Inner margins of eyes very weakly convergent so that lower face appears almost square, the eyes separated by at least a distance of 0·8 times the length of face from antennal base to clypeal apex (Text-fig. 234); epicnemial carina medio-ventrally raised into a weak flange, but this flange does not extend anteriorly between fore coxae; genal carina reaching base of mandible separated from hypostomal carina (sometimes there is an auxillary carina present which crosses hypostomal carina); hindwing with *Rs* and *M* distinct almost to wing margin.

Flagellum usually very elongate, obviously longer than remainder of insect. (Ethiopian region) . . . . ***BIMENTUM*** Townes (p. 77)

– Inner margins of eyes moderately convergent ventrally so that lower face is distinctly longer than broad, the eyes separated by, at the most, a distance of 0·72 times the length of face from antennal base to clypeal margin; epicnemial carina medio-ventrally raised into a tooth-like projection which extends anteriorly between the bases of the fore coxae (Text-fig. 222); genal carina either joining hypostomal carina, or reaching base of mandible contiguous with hypostomal carina; hindwing with *Rs* and *M* not pigmented to wing margins 35

35 (34) Forewing with intercubital index greater than 1·0; marginal index less than 2·2; hindwing with radial index greater than 0·8; hind tarsi of ♂ strongly swollen. (Mediterranean region) . . . . ***ATROMETUS*** Foerster (p. 75)

– Forewing with intercubital index less than 0·70; marginal index greater than 2·5; hindwing with radial index less than 0·7; hind tarsi of ♂ not swollen.

Usually yellow species with black markings. (Oriental region) ***CLATIIA*** Cameron (p. 74)

36 (29) Occipital carina separated from posterior ocelli by at least 3·0 times the diameter of an ocellus; apex of clypeus with a pair of teeth or weak tubercles medianly. (Nearctic region) . . . . ***METOA*** Townes (p. 73)

– Occipital carina close to posterior ocelli, at most separated by about 1·5 times the diameter of an ocellus; apex of clypeus with a single median apical tooth 37

37 (36) Eye surface bearing long hairs, the hairs being longer than the distance separating them basally; fore tibial spur usually with less than 12 widely spaced subacuminate macrotrichia on inner face.

♀ with valvula 3 as long as or longer than tergite 2; ♂ with distivolsella with a central hump bearing elongate spines. (Cosmopolitan) ***TRICHOMMA*** Wesmael (p. 63)

– Eye surface glabrous or if rarely with hairs then the hairs are short, basally separated by more than thrice their length; fore tibial spur with numerous closely packed acute macrotrichia on inner face 38

38 (37) Flagellar segments 1–5 very elongate, segment 4 about 7·0 times as long as broad; hindwing with radial index less than 0·4; posterior corner of pronotum with weak to strong longitudinal flanges (Text-fig. 203); posterior transverse carina of mesosternum present only laterally as vestiges.

♂ with distivolsella bearing long spines centrally positioned (Oceanic region) . . . . . ***SPOLAS*** Townes (p. 72)

– Flagellar segments 1–5 not unusually elongate, segment 4 at very most 5·0 times as long as broad; hindwing with radial index more than 0·5; posterior corner of pronotum without flanges 39

39 (38) Forewing with 1*m–cu* and Cu_{1a} basally united into a distinct short common stalk, or arising from same point on Cu_1; ♀ with ovipositor hastate, without a subapical dorsal notch; ♂ with aedeagus laterally slender, and in dried specimens, acutely pointed. (All regions except Australian) . ***PARANIA*** Morley (p. 70)

– Forewing with 1*m–cu* and Cu_{1a} basally separated by a short to moderately long abscissa of Cu_1; ♀ with ovipositor with a more or less distinct subapical dorsal notch; ♂ with aedeagus apically truncate or bluntly rounded . . . 40

40 (39) Forewing with cubital index 0·75 or greater; posterior transverse carina of mesosternum interrupted in front of each mid coxa.

♂ with aedeagus obliquely truncate. (Holarctic)

HABRONYX subgenus ***CAMPOSCOPUS*** Foerster (in part) (p. 37)

– Forewing with cubital index 0·60 or less, usually very much less; posterior transverse carina of mesosternum usually complete. (Cosmopolitan)

AGRYPON Foerster (few species) (p. 66)

41 (3) Wings with venation very reduced; forewing with 2*m–cu* absent (Text-fig. 200); gaster very elongate; thorax clothed with dense whitish pubescence.

Gonosquamae of ♂ elongate (Text-fig. 93). (Neotropical region)

OPHIONELLUS Westwood (p. 82)

– Wings without reduced venation, except possibly in the distal veins of the hindwing; forewing with 2*m–cu* present; gaster not unusually elongate; thorax with scattered inconspicuous pubescence 42

42 (41) Hindwing with distal abscissa of Cu_1 totally absent; forewing with 1*m–cu* and Cu_{1a} basally united into a short common stalk; hind tibial spurs inserted before apex of tibia. (Nearctic region) . . ***CALCANEUM*** Townes (p. 74)

– Hindwing with distal abscissa of Cu_1 present; forewing with 1*m–cu* and Cu_{1a} basally separated by an abscissa of Cu_1; hind tibial spurs inserted at apex of tibia 43

43 (42) Lower anterior margin of pronotum with a large tooth (Text-fig. 205); hind tarsal claws sharply angled more than 100° (Text-fig. 221) 44

– Lower anterior margin of pronotum without a tooth; hind tarsal claws curved weakly to moderately (Text-fig. 215) 45

44 (43) Mesoscutum with a transverse suture before the scuto-scutellar groove; forewing with 2 + 3*rm* widely separated from 2*m–cu* (Text-figs 198, 199); hindwing with 7 widely spaced hamuli on R_1.

Propodeum globosely swollen; fore coxae with a transverse carina on ventral surface. (Eastern Palaearctic) . ***BRACHYNERVUS*** Uchida (p. 78)

– Mesoscutum without a transverse suture before the scuto-scutellar groove; forewing with 2 + 3*rm* proximal to 2*m–cu* by about its own length; hindwing with about 12 closely interspaced hamuli on R_1.

Head behind the eyes abruptly narrowed (Text-fig. 176). (Malaysian)

Heteropelma perornatum Cameron (p. 52)

(This species sometimes has the inner tibial spur very reduced and although it appears to have a single spur on mid tibia, two are in fact present.)

45 (43) Clypeus elaborately sculptured (Text-fig. 167); mandible bidentate; tarsal

claws small, basally pectinate; occipital carina centrally interrupted by a series of discontinuities. (Turkey). ***CLYPEOCAMPULUM*** gen. n. (p. 42)

– Clypeus smooth; mandible unidentate; tarsal claws long, weakly curved, not pectinate; occipital carina complete. (Western Nearctic) ***LIOPTERNA*** Townes (p. 48)

The described final instar larvae of Anomaloninae

The characters used in this key were found to work for the material available. However, one genus, *Agrypon*, was found to contain species with widely differing larval morphology. Whether this is because *Agrypon* contains a number of species which are not as closely interrelated as their adult morphology has led workers to believe, or because the characters used for the larva are not constant within a genus is not clear. Only by examination of a large amount of larval material can this problem be solved. It is apparent, however, that the massive sclerotization of the epistoma and pleurostoma, which has been used for dividing the Therionini into two tribes, occurs in species belonging to both these groups and cannot therefore be used as a tribal character. As this massive sclerotization has only been observed in larger Therionini (*Heteropelma*, *Therion*, *Habronyx* (*Habronyx*) and *Encardia*) it is possible that the size of the insect is important in determining the relative degree of sclerotization of the epistoma etc.

1 Blade of mandible with teeth (Text-fig. 141); setae present on prelabium ***ANOMALON***

– Blade of mandible without teeth; prelabium without setae 2

2 (1) Distal end of stipital sclerite bifid; hypostoma short, about 1·3 times as long as basal width of mandibles . . . . . ***TRICHOMMA***

– Distal end of stipital sclerite not bifid; hypostoma short to very long . . 3

3 (2) Labral sensillae arranged in two clusters on separated sclerotized regions (Text-figs 142, 143, 146). 4

– Labral sensillae arranged in a single group (Text-figs 144, 147) or if with tendency to form two clusters (as in *Barylypa*) then clusters united on a single sclerotized region 8

4 (3) Proximal 0·5 of hypostoma slender, less broad than width of mandible base, parallel-sided throughout most of its length (Text-fig. 151); pleurostoma slender, at very most as broad as basal width of mandible 5

– Proximal 0·5 of hypostoma broader than width of mandible base, strongly tapered for most of its length (Text-fig. 143); pleurostoma broader than basal width of mandible 6

5 (4) Mandibles with blade arising from ventral surface; epistomal arch and pleurostomae very arched so that distance between posterior pleurostomal processes is about equal to distance from median point of a line joining the posterior pleurostomal processes to centre of epistomal arch (Short, 1959 : fig. 62A) ***ATROMETUS***

– Mandibles with blade arising from centre; epistomal arch and pleurostomae moderately arched so that distance between posterior pleurostomal processes is very much less than distance from median point of a line joining the posterior pleurostomal processes to centre of epistomal arch (Text-fig. 151) ***AGRYPON*** (in part)

6 (4) Head sclerites, when viewed flattened on a slide, with distal end of hypostoma

curved and reaching below level of lower margin of silk press; hypostoma longer than 2·5 times basal width of mandible; mandibles with blades arising from centre (Text-fig. 146) . . . . . ***PERISPHINCTER***

– Head sclerites, when viewed flattened on a slide, with distal end of hypostoma not curved or moderately curved so that distal ends do not extend below the level of the silk press; hypostoma shorter than 2·0 times basal width of mandible; mandibles with blades arising from ventral surface . . . 7

7 (6) Ventral part of labial sclerite lightly sclerotized so that labial sclerite appears continuous (Text-fig. 142); hypostoma with distal end curved downwards ***HETEROPELMA***

– Ventral part of labial sclerite not sclerotized so labial sclerite appears to be separated into a pair of lateral parts (Text-fig. 143); hypostoma with distal end not at all curved . . . . . ***THERION***

8 (3) Width of epistoma along entire length and width of pleurostoma along entire length equal to or greater than width of base of mandible; hypostoma shorter than length of mandible from apex of blade to base; hypostomal spur absent entirely; upper ends of labial sclerite broadened (Text-fig. 155) . ***ENCARDIA***

– Width of epistoma in part or width of pleurostoma, in part, less than width of mandible base or with hypostoma longer than 1·5 times length of mandible; hypostomal spur absent or present; upper ends of labial sclerite not obviously broadened 9

9 (8) Silk press with pigmented region crescent-shaped (Text-fig. 148); labral sensillae arranged on a region that has centre and lateral extremities swollen; epistomal arch dorsally raised into a central hump ***HABRONYX (AUSTRANOMALON)***

– Silk press with pigmented region simply U-shaped; labral sensillae arranged on a region that is transversely parallel sided; epistomal arch various . . 10

10 (9) Hypostomal spur present as a small process close to base of posterior pleurostomal process (Text-figs 144, 147) 11

– Hypostomal spur entirely absent 12

11 (10) Hypostoma and pleurostoma very broad, sickle-shaped (Text-fig. 144); distal end of hypostoma acutely pointed . . ***HABRONYX (HABRONYX)***

– Hypostoma and pleurostoma of moderate breadth, almost straight (Text-fig. 147); hypostoma with distal end truncate ***GRAVENHORSTIA (ERIGORGUS)***

12 (10) Hypostoma at extreme proximal end less than 0·7 times as broad as basal width of mandible; pleurostoma at narrowest point less than 0·5 times as broad as basal width of mandible 13

– Hypostoma at extreme proximal end more than 0·9 times as broad as basal width of mandible; pleurostoma at narrowest point more than 0·5 times as broad as basal width of mandible 14

13 (12) Blade of mandible arising from ventral surface of mandible base; hypostoma weakly curved about 40° (Text-fig. 140) . ***HABRONYX (CAMPOSCOPUS)***

– Blade of mandible arising from middle of base; hypostoma evenly but strongly curved through about 80° (Short, 1959 : fig. 62B) . . ***AGRYPON*** (in part)

14 (12) Head sclerites, when viewed mounted flat, with hypostoma weakly curved about 50° so that distal end of hypostoma does not extend below the level of the silk press (Short, 1959 : fig. 61B) . . . . . ***BARYLYPA***

– Head sclerites, when viewed mounted flat, with hypostoma strongly angled about 90° or more and with distal end of hypostoma extending below the level of the silk press 15

15 (14) Epistomal arch centrally acutely angled (Text-fig. 149) . . ***PARANIA***

– Epistomal arch evenly convex 16

16 (15) Width of epistomal arch medianly about equal to the width of the mandible base (Text-fig. 150) . . . . . ***APHANISTES***

– Width of epistomal arch medianly less than 0·8 times the width of mandible base . . . . . ***AGRYPON*** (in part)

Tribe **THERIONINI** Viereck

[Anomaloidae Foerster, 1868 : 140. Type-genus: *Anomalon* Panzer. Based on Gravenhorst's (1829 : 641) misinterpretation of *Anomalon* Panzer.]
[Anomalina Foerster; Thomson, 1887 : 1048.]
[Anomalonini Ashmead, 1894 : 277.]
[Anomalinae Foerster; Dalla Torre, 1901 : 155.]
Pharsaliinae Szépligeti, 1905*a* : 3. Type-genus: *Pharsalia* Cresson (= *Ophionellus* Westwood).
Pharsaliini Szépligeti; Schmiedeknecht, 1908 : 1409.
[Anomalides Foerster; Morley, 1913*a* : 49.]
Hymenopharsalina Viereck, 1918 : 72. Type-genus: *Hymenopharsalia* Morley (= *Ophionellus* Westwood).
Therioninae Viereck, 1918 : 72. Type-genus: *Therion* Curtis.
Ophionellini Cushman, 1922 : 16. Type-genus: *Ophionellus* Westwood.
Ophionellina Cushman; Townes, 1945 : 710.
Ophiopterina Townes, 1945 : 711. Type-genus: *Ophiopterus* Brullé.
Aphanistina Townes, 1945 : 711. Type-genus: *Aphanistes* Foerster.
Therionina Viereck; Townes, 1945 : 723.
Therionini Viereck; Hellén, 1950 : 31.
Gravenhorstina Hellén, 1950 : 31. Type-genus: *Gravenhorstia* Boie. **Syn. n.**
Trichommina Hellén, 1950 : 31. Type-genus: *Trichomma* Wesmael.
Gravenhorstiina Townes, 1951 : 396.
Gravenhorstiini Townes; Short, 1959 : 502.
Erigorgina Viktorov, 1968 : 554. Type-genus: *Erigorgus* Foerster.
Podogastrini Townes, 1971 : 148. Type-genus: *Podogaster* Brullé. **Syn. n.**
Theriini Townes, 1971 : 155.

For the diagnostic characters of the tribe see Table 3 (p. 93).

Strict application of the Law of Priority would favour Pharsaliini as the name of this tribe, but I have followed other recent authors (Perkins, 1959; Viktorov, 1968) in preferring the name Therionini because of its much wider use. This spelling, rather than the recently corrected form, Theriini, is used in accordance with Article 29(d) of the *International Code of Zoological Nomenclature*.

Genus ***HABRONYX*** Foerster

Habronyx Foerster, 1868 : 145.

Eye without, or rarely with, short scattered pubescence; inner margins of eyes weakly to moderately convergent ventrally; occipital carina complete, usually closer to the posterior ocelli than the diameter of an ocellus, except in some Oriental species; frons with or without a median vertical carina (in one Australian species with a median vertical lamella present). Antennae moderately long, those of ♀ without a white band; scape truncate, about 2·0 times as long as pedicel; fourth flagellar segment about 2·0 times as long as broad. Clypeus with, or rarely without, a median apical tooth; mandibles bidentate, apex not twisted, upper tooth distinctly the longer; labial palp with four or very rarely three segments; cardo basally lobed. Genal carina reaching base of mandible.

Pronotum dorsally long, subhorizontal, with a transverse groove; lower anterior margin of pronotum without a tooth (except in one Palaearctic species); lower anterior corner acute to truncate. Anterior of mesoscutum rather evenly to abruptly rounded in profile, without an apical concavity present (except in one Palaearctic species); notauli weakly to strongly impressed, extending beyond the centre of the mesoscutum in most species, and with medio-posterior region of mesoscutum rugosely sculptured; transverse suture of the mesoscutum absent, transverse furrows absent. Epicnemial carina various, medio-ventrally not raised into a flange; sternaulus indistinct or absent; posterior transverse carina of mesosternum interrupted in front of each mid coxa.

Fore coxa smooth; fore tibial spur with numerous acute macrotrichia on inner face. Mid tibia with two spurs. Hind trochanter various, between 0·8 and 1·9 times as long as trochantellus; hind tarsi of ♂ not swollen; hind tarsal claws various, from almost not to noticeably sexually dimorphic.

Forewing with *Rs* sinuate to straight; 2 + 3*rm* distal, opposite or proximal to *2m–cu*; 1*m–cu* and Cu_{1a} basally separated. Hindwing with 9–19 hamuli on R_1; distal abscissa of Cu_1 present, very rarely indistinct basally.

Propodeum reticulate; spiracle various, usually 1·4–2·4 times as long as broad; apex of propodeum reaching about 0·35 times the length of hind coxa. Gaster elongate.

♀ genitalia. Valvula 3 a little shorter than the apical abdominal depth or at most 0·6 times as long as tergite 2; apex of ovipositor constricted, the constricted part 4–6 times as long as the median thickness of ovipositor; extreme apex straight; ovipositor weakly to moderately laterally compressed.

♂ genitalia. Syntergites separated by a median dorsal longitudinal membranous area. There is considerable variation in the morphology of the male genitalia. This variation is more fully discussed below.

Recently *Habronyx* has been extended to include several previously distinct genera (Townes, 1971), but the inclusion of certain species is not accepted by all workers (Horstmann, 1972). A detailed study of the species has shown that there are four distinct species-groups, at least two of which are closely related.

The *Habronyx heros* species-group includes ten species originally placed in three separate genera, *Habronyx*, *Acanthostoma* and *Macrostemma*. There is considerable morphological variation within this group, but when all species are examined it is apparent that there is no real discontinuity within the ranges of variation, and consequently the inclusion of this group of species together is acceptable.

It has recently been possible to examine the cephalic capsule of the final instar larva of *Habronyx* sp. (*?pyretorus*) (the adult specimen is somewhat damaged so specific determination was not possible). The cephalic capsule was observed to be quite distinct from that of the *Habronyx nigricornis*-group in having a massive pleurostoma and hypostoma but a rather weakly sclerotized epistomal arch. A small but clearly discernible hypostomal spur was found to be present (Text-fig. 144). Previous authors (Short, 1959; Townes, 1969) have characterized the Anomaloninae by the complete lack of a hypostomal spur, but not only has a small hypostomal spur been found within some species referable to this genus but a vestigial hypostomal spur has been observed in some species of *Gravenhorstia*.

There is a marked variation in the form of the aedeagus between species within the *heros*-group. All species examined were found to have the aedeagus with a fairly heavily sclerotized dorsal region with a well developed anterio-dorsal membrane bearing a few weak spines. A ventral membranous area covered with spines

was also observed to be present. The extent of the anterio-dorsal and ventral membranous areas were found to be characteristic of the species examined (*H. heros*, *H. insidiator*, *H. australasiae*, *H. pyretorus* and *H. orbitalis*). In *H. heros* the anterio-dorsal membrane does not extend on to the apical face of the aedeagus, and the ventral membranous area is large and reaches the aedeagal apex (Text-fig. 100). There is a reduction in the size of the ventral membranous area through the species *H. orbitalis*, *H. insidiator*, and this area is most reduced in *H. pyretorus* (Text-figs 102–104). In this latter species there is an extension of the aedeagus along the ventral margin of the anterio-dorsal membrane which extends medio-vertically across the aedeagal apex. *H. australasiae* was observed to be somewhat unusual in having the anterio-dorsal membrane produced into a hook-like prominence (Text-fig. 105). In no species was there found to be a lateral extension of the ventral membranous area.

It is possible to correlate the reduction in the size of the ventral membranous area of the aedeagus with other characters such as the shape of the tarsal claws (those of *H. heros* are abruptly curved and pectinate almost to the apices whilst those of *H. pyretorus* are long, weakly curved and pectinate only at the extreme bases) and the shape of the propodeum (that of *H. heros* is about 1·1 times as long as broad, whereas that of *H. pyretorus* is about 0·8 times as long as broad). This correlation of characters provides strong evidence about the interrelationships and possible lines of evolution that have occurred within this group.

A second species-group, the *nigricornis*-group, was previously accorded separate generic status. These species are distinct from the aforementioned species-group in a number of characters (Table 1). It is possible that certain differences, such as the form of vein *Rs* in the forewing, may be the result of differences in the sizes of the insects concerned (*heros*-group are large insects of 25 mm+, whereas the *nigricornis*-group are considerably smaller, less than 15 mm). In the *heros*-group the labial palps are composed of four distinct segments, but in some smaller specimens of the *nigricornis*-group the labial palps have only three distinct segments, the fourth is apparently fused with the apex of the third. Similar fusion of third and fourth palpar segments has been observed in other Therionine genera, notably *Agrypon*, where larger individuals have four distinct palpar segments, but small specimens of the same or a closely related species have only three palpar segments. Examination of a long series of specimens of varying size revealed that there is an increasing degree of fusion between the two apical segments of the labial palps as there is a decrease in the size of the individuals examined (Text-figs 243–245). It must be noted however that size need not necessarily be the only factor affecting palpar fusion, for in the genus *Encardia* there is considerable atrophication of the segments of both the labial and maxillary palps in large insects (Text-fig. 242).

Measurement of the cubital index in a group of specimens gave the results shown in Chart 1. It can be seen that there is almost no overlap between the two groups.

A study of the male genitalia revealed that the *nigricornis*-group is closely related to the *heros*-group. The distivolsellae of the two species-groups are relatively similar in being elongate and bearing a very distinct diagonal spinose ridge (Text-fig. 68). The aedeagi of the *nigricornis*-group have apico-dorsal membranes which

do not extend on to the aedeagal apices, are less sclerotized and bear pairs of detached sclerites in the membranes (Text-fig. 101). The aedeagi have few spines and bear a number of apically impressed tubercles which appear to have a minute apical pore. The ventral membranous areas are without spines and are laterally extended into small flanges.

The nomenclature of the *nigricornis*-group is particularly confused. Recently, before being included within *Habronyx*, this group was accorded separate generic status as *Camposcopus* (Townes *et al.*, 1965).

A number of authorities have treated *Camposcopus*, *Labrorychus* and *Blaptocampus* as separate genera. *Anomalon nigricorne* is the type-species of both *Labrorychus* (as included by Brischke, 1881) and *Blaptocampus* (as designated by Viereck, 1914*a*). The former must therefore take precedence. However *Labrorychus* has been extended by later European authors (Schmiedeknecht, 1908; 1936; Morley, 1915; Hellén, 1950; Ceballos, 1963) to include species not congeneric with the type-species, and often the type-species was placed in *Blaptocampus* as a separate genus. These incorrectly placed species differ from *A. nigricornis* in having a distinct transcarina on the fore coxae and in having vein Cu_{1a} basally very close to *1m–cu*. These species have subsequently more correctly been included within the genus *Trichionotus* by Townes *et al.* (1965).

The genus *Camposcopus*, type-species *C. aclerivorus* Rowher (included by Rowher, 1915) has been distinguished from the group containing *nigricornis* solely by the fact that the third maxillary palpar segment is swollen in the former species, but not in the latter. In personal communication, Dr Townes suggested that the shape of the maxillary palp might be a sexually dimorphic feature, being more slender in the female of the species.

Horstmann (1972) observed that there is a considerable degree of variation in the shape of the third maxillary palpar segment, and did not consider this feature warranted generic distinction.

Examination of a number of specimens of *A. nigricorne* has shown that although the majority of specimens have the third maxillary palpar segment quite elongate, about 3·0 times as long as broad, a few males differ solely in having this segment much stouter, between 2·1 and 2·4 times as long as broad. It is apparent therefore that *Labrorychus* and *Blaptocampus* must be included as synonyms of *Camposcopus*.

The species described as *Anomalon biguttatum* has in the past presented some difficulty as to where it should most suitably be placed. Older authors placed it within the genus *Erigorgus*. Schmiedeknecht considered this species was intermediate between *Erigorgus* and *Aphanistes*. Morley concurred with this opinion and subsequently included *Aphanistes* and *A. biguttatum* within *Erigorgus*. More recently Townes (1971) included this species within *Habronyx*.

An examination of the critical features indicated that *A. biguttatum* is distinct from other species-groups in having a unique combination of characters (Table 1).

The form of the male genitalia of *A. biguttatum* is quite distinct from that of other groups of *Habronyx* species. The gonolacinia is rather straight and elongate (Text-fig. 51) and the distivolsella is somewhat quadrate with a weakly impressed diagonal ridge (Text-fig. 72). The aedeagus is terminally weakly bilobate with

Table 1

Comparison of the subgenera of *Habronyx*

HABRONYX (*HABRONYX*)	*HABRONYX* (*CAMPOSCOPUS*)	*HABRONYX* (*HABROCAMPULUM*)	*HABRONYX* (*AUSTRANOMALON*)
Cephalic capsule of larva with epistoma very broad; hypostomal spurs present.	Cephalic capsule of larva with epistoma very slender; hypostomal spurs absent.	Unknown.	Cephalic capsule of larva with epistoma moderately broad; hypostomal spurs absent.
Metanotum not unusually broad; postscutellum broader than long; propodeum less than 1·4 times as long as broad.	Metanotum not unusually broad; postscutellum broader than long; propodeum about 1·4 times as long as broad.	Metanotum broad, postscutellum much longer than broad; propodeum about 2·0 times as long as broad.	Metanotum not unusually broad, postscutellum broader than long or quadrate; propodeum less than 1·5 times as long as broad.
Tarsal claws pectinate or simple, moderately large, usually strongly curved, not markedly sexually dimorphic.	Tarsal claws pectinate at least basally, small to moderately large, evenly curved, not markedly sexually dimorphic.	Tarsal claws of ♀ basally pectinate, those of ♂ longer, less strongly curved, simple.	Tarsal claws basally pectinate or simple, those of ♂ long and weakly curved, those of ♀ shorter and more strongly curved.
Wings with CI = 1·3–1·8, MI = 1·2–1·5, NI = 0·5–2·0.	Wings with CI = 0·7–1·3, MI = 1·6–2·1, NI = 3·5+.	Wings with CI = 0·8–1·0, MI = 1·5–1·7, NI = 0·8–1·0.	Wings with CI = 1·0–1·9, MI = 1·2–1·5, NI = 0·9–1·4.
Hind trochanter 1·5–2·0 times as long as trochantellus.	Hind trochanter 1·2–1·5 times as long as trochantellus.	Hind trochanter 0·9–1·1 times as long as trochantellus.	Hind trochanter 0·9–1·5 times as long as trochantellus.
Distivolsella slender, distally swollen.	Distivolsella slender, distally swollen.	Distivolsella almost quadrate, flattened.	Distivolsella almost quadrate, flattened.

the ventral and dorsal membranous areas united apically. The dorsal region of this membrane bears a number of tubercles, whilst the ventral region is devoid of any obvious sculpture except for scattered spines at the extreme basal corner (Text-fig. 106). Dorsally the aedeagus is fairly heavily sclerotized but there is an indistinctly defined membranous area on the extreme dorsal margin of the central region, near the angulation. The aedeagus does not have the ventral area laterally extended.

There are in the collections of the BMNH and the Australian National Insect Collection a series of specimens which represent a series of closely interrelated species. This group of species is difficult to place as in some features it is intermediate between *Habronyx* and *Gravenhorstia* (*Erigorgus*). For the present this group is retained as a separate subgenus of *Habronyx* on account of having the notauli distinct, although they are very weak in some species.

As *Habronyx* contains four distinctive species-groups it is suggested that it be subdivided into four subgenera, *H.* (*Habronyx*), *H.* (*Camposcopus*), *H.* (*Habrocampulum*) and *H.* (*Austranomalon*). This system of classification, that is the division of a genus into four subgenera, may seem an unnecessary complication in the taxonomy of an already complex group. The Therionini are a large group of morphologically rather uniform species, and there are few characteristics that are specific to any one genus. In consequence there has often been a genus erected on the basis of a single or relatively few more obvious features, and certain genera are more easily definable by their lack of characters (such as frontal lamellae, hirsute eyes, unicalcarate mid tibiae or carinate fore coxae) than they are by positive features. As a result a range of rather heterogeneous species have come to be included within some genera. Examination of a large number of characteristics and consideration of the combinations of these features clearly showed that the proposed subgenera are quite distinct from one another, and that the status of these groups as subgenera is in keeping with the taxonomy of the group as a whole.

Subgenus ***HABRONYX*** Foerster

Habronyx Foerster, 1868 : 145. Type-species: *Habronyx gravenhorstii* Foerster, 1868 : 148 [= *Anomalon heros* Wesmael, 1849 : 125], by monotypy.

Acanthostoma Kriechbaumer, 1895 : 128. Type-species: *Acanthostoma japonicum* Kriechbaumer, 1895 : 129 [= *Anomalon insidiator* Smith, 1874 : 396], by monotypy.

Macrostemma Shestakov, 1923 : 46. Type-species: *Macrostemma elegans* Shestakov, 1923 : 46, by monotypy.

Formosanomalon Uchida, 1928 : 241. Type-species: *Formosanomalon baibarense* Uchida, 1928 : 241, by monotypy.

Inner margins of eyes subparallel; inter-ocellar distance 0·8–1·0 times as long as orbital ocellar distance; frons with or without a median vertical carina, rarely with a lamella. Clypeal apex rounded with a moderate to large median tooth. Genae broad to narrow, head often very buccate; genal carina joining base of mandible and separated from hypostomal carina.

Pronotum with lower corner acutely pointed, without an anterior tooth. Mesoscutum in profile angularly rounded, without an apical concavity. Epicnemial carina long to absent, if short then with upper end remote from hind margin of pronotum, if long then seldom with upper end reaching hind margin of pronotum. Scutellum flat to convex, punctate, reticulate

or coriaceous; postscutellum short, much broader than long, convex. Propodeum from moderately long to short and swollen.

Tarsal claws moderate to long, from almost completely to only basally pectinate.

Forewing with first subdiscal cell explanate distally; vein *Rs* sinuate. Hindwing with 13–19 hamuli on vein R_1.

CI = 1·35–1·72; BI = 1·55–2·10; DBI = 0·60–0·85; RI = 1·60–2·00; NI = 0·59–2·00; ICI = 2·60+; MI = 1·20–1·48; PI = 3·50–5·00.

♂ genitalia. Ninth abdominal sternite transverse, posteriorly truncate; gonosquamae short. Gonolaciniae abruptly angled about 60° distally; teeth large; apodeme straight, extending 0·5 times the length of basivolsellar strut. Distivolsella slender, basally about 0·5 times as wide as long; clasping surface concave, distally swollen with teeth diagonally arranged on proximal face of swelling. Proximal end of paramere simply acute; ergots large and conspicuous. Aedeagus in profile various, but with separate dorsal and ventral membranous areas, the latter spinose and not laterally extended; lateral sclerotized region of aedeagus usually reaching distal apex (Text-figs 68, 87, 100, 102–105).

DISTRIBUTION. Species of this subgenus are recorded from the Palaearctic, Oriental, Australian and Neotropical regions. An undescribed species is known from southern Africa.

INCLUDED SPECIES. Specimens of the following have been examined and found referable to this subgenus:

H. (*Habronyx*) *heros* (Wesmael), *H.* (*Habronyx*) *orbitalis* (Morley) **comb n.**, *H.* (*Habronyx*) *pyretorus* (Cameron), *H.* (*Habronyx*) *australasiae* (Morley) **comb. n.**, *H.* (*Habronyx*) *fulvipes* Townes, Momoi & Townes, *H.* (*Habronyx*) *regalis* (Morley), *H.* (*Habronyx*) *elegans* (Shestakov) and *H.* (*Habronyx*) *baibarense* (Uchida).

Subgenus *CAMPOSCOPUS* Foerster **stat. n.**

Camposcopus Foerster, 1868 : 145. Type-species: *Camposcopus aclerivora* Rowher, 1915 : 226, by monotypy.

Labrorychus Foerster, 1868 : 146. Type-species: *Anomalon nigricorne* Wesmael, 1849 : 126, by monotypy.

Blaptocampus Thomson, 1892 : 1765. Type-species: *Anomalon nigricorne* Wesmael, 1849 : 126, by subsequent designation (Viereck, 1914*a* : 22).

Inner margins of eyes ventrally convergent; inter-ocellar distance 1·1–1·2 times as long as orbital ocellar distance; frons with or without a strong median vertical carina. Clypeal apex pointed, with a small median tooth. Genae narrow, head never posteriorly buccate; genal carina joining base of mandible contiguous with hypostomal carina.

Pronotum with lower corner truncate, without a tooth. Mesoscutum in profile angularly rounded, without an apical concavity. Epicnemial carina long, upper end joining hind margin of pronotum above the centre of mesopleuron. Scutellum flat, weakly coriaceous; postscutellum short, much broader than long, very convex. Propodeum long, not swollen.

Tarsal claws short, not longer than arolium, pectinate almost to apices.

Forewing with first subdiscal cell not explanate distally; vein *Rs* not sinuate. Hindwing with 9–12 hamuli on vein R_1.

CI = 0·75–1·25; BI = 1·10–1·49; DBI = 0·60–0·70; RI = 1·40–1·60; NI = 3·50+; ICI = 1·30–1·65; MI = 1·60–2·10; PI = 2·50–3·30.

♂ genitalia. Ninth abdominal sternite transverse, posteriorly truncate; gonosquamae short. Gonolaciniae abruptly angled about 90° distally; teeth small; apodeme straight, extending 0·5 times the length of basivolsellar strut. Distivolsella slender, basally about 0·4 times as wide as long; clasping face concave with distal end swollen, the swollen end bearing peripheral

spines. Paramere proximally simply rounded. Aedeagus in profile sinuate, apically truncate, with separate dorsal and ventral membranous areas, the latter not spinose but laterally extended into triangular flanges; lateral sclerotized region of aedeagus reaching distal apex, bearing blunt tubercles (Text-figs 60, 101).

Distribution. Species of this subgenus are recorded from all regions except the Ethiopian and Neotropical.

Included species. Specimens of the following have been examined and found referable to this subgenus:

H. (*Camposcopus*) *nigricornis* (Wesmael), *H.* (*Camposcopus*) *aclerivorus* (Rowher), *H.* (*Camposcopus*) *canaliculatus* (Holmgren), *H.* (*Camposcopus*) *perspicuus* (Wesmael), *H.* (*Camposcopus*) *tonnaiensis* (Uchida), *H.* (*Camposcopus*) *maidan* (Shestakov), *H.* (*Camposcopus*) *sonani* (Uchida) and *H.* (*Camposcopus*) *maxillaris* (Uchida).

Subgenus ***HABROCAMPULUM*** **subgen. n.**

Type-species: *Anomalon biguttatum* Gravenhorst, 1829 : 642.

Inner margins of eyes weakly convergent ventrally; inter-ocellar distance 1·1–1·3 times as long as orbital ocellar distance; frons with a weak median vertical carina. Clypeal apex weakly rounded with a small median tooth. Genae narrow, head not buccate; genal carina reflexed weakly, joining hypostomal carina at mandibular base.

Pronotum with lower corner obliquely truncate, with a distinct tooth near the anterior corner. Mesoscutum in profile evenly but rather abruptly rounded with a small concavity near the apical margin. Epicnemial carina short, upper end angled to meet lower corner of pronotal margin. Scutellum very convex, punctate; postscutellum much longer than broad, weakly convex. Propodeum very elongate, 2·0 times or more as long as broad centrally; basally almost parallel sided.

Tarsal claws not long, indistinctly pectinate basally (more so in ♂ than ♀) (Text-figs 219, 220).

Forewing with first subdiscal cell distally explanate; *Rs* not sinuate; hindwing with 10–12 hamuli on R_1.

Cl = 0·80–1·10*; BI = 1·45–1·80*; DBI = 0·55–0·65*; MI = 1·50–1·70*; RI = 1·25–1·55*; NI = 0·80–1·00*; ICI = 1·20–1·35*; PI = 2·40–2·90*.

♂ genitalia. Ninth abdominal sternite transverse, posteriorly truncate; gonosquamae short. Gonolacinia slender, distally weakly angled about 30°; teeth of moderate size; apodeme straight, extending 0·6 times the length of basivolsellar strut. Distivolsella moderately broad, basally 0·6 times as wide as long; clasping face concave with peripheral ridge bearing spines. Paramere proximally simply acute. Aedeagus in profile weakly angled, apically rounded, with dorsal and ventral membranous areas confluent apically, the latter neither spinose nor laterally extended; lateral sclerotized region of aedeagus not reaching distal apex (Text-figs 51, 72, 106).

As this subgenus is known only from a little material, and as it does not have any obvious affinities with other Therionini, the author has chosen to retain it within *Habronyx* as suggested by Townes (1971) although it has been accorded separate subgeneric distinction. The above descriptions, and the dendrogram (Text-fig. 249) clearly indicate that this species is not very closely related to either of the preceding subgenera, and it is quite possible that when more material is available this subgenus may be accorded separate generic status.

DISTRIBUTION. This subgenus is only recorded from the western Palaearctic Region.

INCLUDED SPECIES. Only one species, the type-species, is at present known to be referable to this subgenus.

Subgenus *AUSTRANOMALON* subgen. n.

Type-species: *Habronyx* (*Austranomalon*) *pammi* sp. n.

Inner margins of eyes subparallel, the eye surface glabrous or with short sparse pubescence; lower face flat. Clypeus weakly produced apically, or rounded, with or without a median apical tooth; mandible subequally bidentate or with lower tooth distinctly the shorter. Genal carina reaching the hypostomal carina at base of mandible; frons with at most an indistinct median vertical carina, often with a median vertical impressed groove.

Pronotum usually with lower corner acute, without a tooth; mesoscutum in profile varying from almost evenly rounded to angularly rounded, with at most an indistinct apical concavity. Epicnemial carina short, usually not extending above lower corner of pronotum, upper end distant from anterior margin of mesopleuron. Propodeum quite short, posteriorly extended about 0·5 times the length of hind coxae.

Tarsal claws long, weakly curved, those of ♀ somewhat shorter, more curved and more extensively pectinate than those of ♂; pecten of claws not extending beyond centre (Text-figs 213, 214).

Forewing with first subdiscal cell distally explanate; *Rs* not or weakly sinuate; hindwing with 10–15 hamuli on vein R_1.

CI = 1·00–1·88; BI = 1·45–2·15; DBI = 0·55–0·75; MI = 1·25–1·45; RI = 1·35–2·20; NI = 0·90–1·40; ICI = 1·00+; TI = less than 1·50.

♂ genitalia. Ninth abdominal sternite transverse; gonosquamae short and truncate. Gonolacinia distally evenly curved about 50°; teeth small; apodeme straight, extending about 0·4 times the length of basivolsellar strut. Distivolsella broad, basally about 0·75 times as wide as long; clasping face flat with a weak peripheral ridge bearing small teeth. Aedeagus in profile medianly angled, apically with a dorsal lobe, dorsally weakly convex; apicodorsal lobe membranous, irregularly delineated proximally; ventral membranous area present, spinose, laterally weakly extended (Text-figs 84–107).

This is not an easy group to define, as it has features not only of *Habronyx* but also of *Gravenhorstia* (*Erigorgus*) and *Barylypa*. From a detailed study of the material in the Australian National Insect Collection, it became apparent that the species of this group are closely interrelated, yet when considered as a whole the group was found to vary in certain characters which are far less variable in species groups from other zoogeographic regions, and have in consequence been used to facilitate generic separation, especially in the western Palaearctic region. The most widely used and apparently invariable character utilized to separate *Habronyx* from *Gravenhorstia* is the shape of the mesoscutum in profile. The present study of species placed in this subgenus has shown that there is an almost continuous gradation from having the mesoscutum angularly rounded with distinctly impressed notauli to having the mesoscutum evenly rounded without notauli. Species with the former facies are included within *Habronyx*, and for the present it is most convenient to include *Austranomalon* species which always have a trace of notauli within *Habronyx*. However, this group of Australian insects are clearly related to *Gravenhorstia* in the form of the male genitalia. The disti-

volsella is almost quadrate and flat, whereas those of *Habronyx* (*Habronyx*) are slender and distally swollen (Text-fig. 68). The aedeagi of *Australanomalon* species are lobed similar to those of *Erigorgus*, although they resemble *Habronyx australasiae* in having the dorsal membranous region irregularly defined proximally (Text-figs 105, 107, 108, 109).

It has been possible to examine the cephalic capsule of the final instar larva of some species of *Habronyx* (*Australanomalon*). The structure of this was found to be very like that of *Gravenhorstia* (*Erigorgus*) and not at all like that of *Habronyx* (*Habronyx*) or *H.* (*Camposcopus*). However, as noted earlier, there is an extremely great difference in the form of the cephalic capsules of these two closely related subgenera, larger species tending to have massively sclerotized hypostomae, epistomae and pleurostomae, whereas small species tend to have disproportionately slender hypostomae etc.

The evaluation of a large number of characters in the phenetic investigation has shown that *Australanomalon* species have more features in common with *Gravenhorstia* than *Habronyx*. However, if *Australanomalon* were included as a subgenus of *Gravenhorstia*, then it would be extremely difficult to define the genus *Gravenhorstia* as a whole and for the present it is most convenient to restrict *Gravenhorstia* to include only the species without any trace of notauli.

Distribution. This subgenus has only been recorded from the Australian region.

Included species. *Habronyx* (*Australanomalon*) *pammi* sp. n.

Habronyx (*Australanomalon*) *pammi* sp. n.

Holotype ♀, Australia: New South Wales, 6·5 km (4 miles) north Batemans Bay, 29.ix.1959 (*E. F. Riek*) (ANIC).

Apex of clypeus evenly rounded with a small median apical tooth (Text-fig. 160); lower mandibular tooth 0·6 times the length of upper, lower margin of mandible basally with a small flange; anterior tentorial pit very ellipsoidal; frons rugose with a weak median vertical impression. Flagellum longer than gaster, with about 60 segments.

Mesoscutum with an indistinct median apical concavity, in profile almost evenly rounded; extreme anterior margin with a pair of latero-median polished triangular areas, remainder of mesoscutum punctate except for the notauli which are weakly impressed, rugose, and extend well beyond the centre of the mesoscutum; scutellum flattened, not laterally carinate.

Forewing with 2 + 3*rm* distal to *2m–cu*; CI about 1·25; hindwing with NI about 0·70.

Ovipositor 0·75 times length of tergite 2.

Head black; lower face usually completely yellow, rarely with a pair of indistinct black marks; mouthparts except for the apices of mandibles, genae for 0·5 of their length and marks on vertex yellow. Antennae blackish, scape ventrally yellow marked.

Thorax black; tegulae, scutellum, occasionally post-scutellum and a central mark on mesoscutum yellow.

Fore and mid legs yellow, the femora and mid coxae infuscate. Hind legs reddish brown to blackish brown, usually with tibia with a subbasal pale band; distal 0·3 of basitarsus and tarsi 2–4 completely yellow.

Abdomen reddish brown; dorsum of tergite 2 black and dorsa of following tergites infuscate.

♂ similar to ♀ but with hind tarsi 2–4 distinctly thickened, ventrally somewhat flattened.

Paratypes. AUSTRALIA: 2 ♀, Australian Capital Territory, Jervis Bay, 7.xi.1956 (*E. F. Riek*) (ANIC); 1 ♂, Tasmania, Freycinet National Park, 28.ii.1963 (*I. Common & M. Upton*) (ANIC); 1 ♀, Queensland, Biggenden, 1–19.xii.1971 (*H. Frauca*) (ANIC); 1 ♀, Brisbane, no further data (*H. Hacker*) (BMNH); 1 ♀, New South Wales, Mt Wilson, 27.ii.1936 (*M. F. Day*) (ANIC); 1 ♂, Queensland, Brisbane, 17.i.1912 (*H. Hacker*) (QM); 1 ♀, Queensland, Bright Valley (*H. W. Davey*) (QM).

Three further described species, all of which are only known from isolated specimens, are also referable to this subgenus. These are *Exochilum robustum* var. *transpositor* Morely, *Exochilum sulcator* Morley and *Laphyctes trilineata* Cameron. *Habronyx* (*Australanomalon*) *transpositor* **comb. n.**, *Habronyx* (*Australanomalon*) *sulcator* **comb. n.** and *Habronyx* (*Australanomalon*) *trilineatus* **comb. n.** are new combinations. At least three further undescribed species, represented in the Australian National Insect Collection, are referable to this subgenus.

Genus *APHANISTES* Foerster

Aphanistes Foerster, 1868 : 145. Type-species: *Anomalon bellicosum* Wesmael, 1849 : 122 by subsequent designation (Viereck, 1914*a* : 13).

Anochilacrum Enderlein, 1921 : 12. Type-species: *Anochilacrum flavigena* Enderlein, 1921 : 12, by original designation.

Eye without pubescence or with sparse scattered hairs, inner margins weakly convergent ventrally to subparallel; occipital carina complete, close to posterior ocelli; frons usually with an inter-antennal lamella. Antennae long, those of ♀ without a white band; scape truncate, about 2·0 times as long as pedicel; fourth flagellar segment about 3·0 times as long as broad. Clypeus with a median apical tooth; mandibles bidentate, apex not twisted, upper tooth distinctly the longer; labial palp with four segments, except in *A. hyalinus* which has three segments; cardo basally lobed. Genal carina joining base of mandible separate from hypostomal carina.

Pronotum dorsally long, subvertical, with a transverse furrow; posterior corner of pronotum twisted, and at most occluding about 0·2 of spiracular sclerite; lower anterior margin without a tooth, lower corner truncate. Anterior of mesoscutum abruptly rounded with an apical concavity; notauli weak, not extending beyond 0·65 times length of mesoscutum; medio-posterior region of mesoscutum punctate; transverse suture of mesoscutum absent, transverse furrows absent. Epicnemial carina various, medio-ventrally not or weakly raised; sternaulus absent; posterior transverse carina of mesosternum interrupted in front of each mid coxa.

Fore coxae smooth; fore tibial spur with numerous acute macrotrichia on inner face. Mid tibia with two spurs. Hind trochanter subequal in length to trochantellus; hind tarsi of ♂ not swollen; hind tarsal claws curved, pectinate to apices, not obviously sexually dimorphic.

Forewing with *Rs* sinuate; 2 + 3*rm* proximal to *2m–cu*; 1*m–cu* and Cu_{1a} basally separated. Hindwing with 10–15 hamuli on R_1; distal abscissa of Cu_1 present.

CI = 1·23–2·10; BI = 1·50–1·90; DBI = 0·47–0·75; MI = 1·30–1·60; RI = 1·90–2·40; NI = 1·40–5·00; ICI = 1·15–1·80; PI = 2·60–3·50.

Propodeum reticulate, spiracle at least 2·0 times as long as broad; apex of propodeum reaching about 0·3 of length of hind coxae. Gaster elongate.

♀ genitalia. Valvula 3 a little shorter than apical abdominal depth; apex of ovipositor constricted, constricted part at least 4 times as long as median thickness of ovipositor; extreme apex weakly decurved; ovipositor weakly laterally compressed (Text-fig. 21).

♂ genitalia. Single syntergum present; ninth abdominal sternite transverse, posteriorly truncate; gonosquamae short. Gonolacinia distally evenly rounded about 80°; teeth small; apodeme straight, extending about 0·25 of length of basivolsellar strut. Distivolsella moderately slender, basally about 0·6 times as wide as long; clasping face concave with teeth arranged

linearly on a transverse ridge. Paramere proximally weakly spatulate, terminally obliquely truncate. Aedeagus in profile angled, apically bilobate, dorsally flattened; dorsal membranous area small, situated on extreme apicodorsal corner; ventral membranous area unusually large, densely spinose, often proximally or proximo-laterally extended; lateral sclerotized region of aedeagus indistinct but reaching to distal apex (Text-figs 44, 73, 112–114).

Aphanistes has customarily been placed close to *Erigorgus* on account of the similarity in the position of vein Cu_{1a} in the forewing, but it would seem that this feature should not be interpreted as indicating a close relationship between the genera.

The form of the genitalia indicates that *Aphanistes* may be quite closely related to *Barylypa* and possibly also *Habronyx* (*Habrocampulum*). This relationship is also suggested by analysis of percentage similarity as represented in the dendrogram (Text-fig. 249).

Distribution. This genus is predominantly Holarctic with a few species recorded from the Indo-Papuan region, one of which, *A. variicolor*, extends into Northern Australia.

Included species. The following species have been examined:

A. hyalinus (Norton), *A. guatemalenus* (Cameron), *A. carinifrons* (Cameron), *A. flavigena* (Enderlein), *A. variicolor* (Morley), *A. villosus* (Tosquinet), *A. bellicosus* (Wesmael), *A. armatus* (Wesmael), *A. coreanus* Uchida, *A. jozankeanus* (Matsumura), *A. ruficornis* (Gravenhorst) and *A. tricolor* Uchida.

Three further undescribed species have also been examined.

Genus ***CLYPEOCAMPULUM*** **gen. n.**

Type-species: *Clypeocampulum tibiale* sp. n.

Eye without pubescence, inner margins parallel; occipital carina not clearly defined, discernible as a discontinuous series of ridges close to posterior ocelli; frons with a median vertical carina. Antennae short, those of ♀ without a white band; scape truncate, about 1·5 times as long as pedicel; fourth flagellar segment about 1·5 times as long as broad. Clypeus moderately pointed without a median apical tooth, unusual in being elaborately sculptured (Text-fig. 167); mandibles bidentate, upper tooth distinctly the longer, apex not twisted; labial palp with four segments; cardo basally lobed. Genal carina joining base of mandible separate from hypostomal carina.

Pronotum dorsally long, subhorizontal, without a transverse groove or furrow; posterior corner of pronotum not occluding spiracular sclerite; lower anterior margin without a tooth, lower corner evenly rounded. Anterior of mesoscutum evenly rounded, without an apical concavity; notauli absent; medio-posterior region of mesoscutum punctate; transverse suture of mesoscutum absent, transverse furrows weakly impressed near posterior margin. Epicnemial carina extending well above lower corner of pronotum, its upper end joining the pronotal margin, medio-ventrally not raised; sternaulus indistinct; posterior transverse carina of mesosternum narrowly interrupted in front of each mid coxa.

Fore coxae smooth; fore tibial spur with numerous acute macrotrichia on inner face. Mid tibia with one spur. Hind trochanter about 1·2 times as long as trochantellus; hind tarsi of ♂ not swollen; hind tarsal claws small, pectinate basally, rather weakly angled near apical 0·7.

Forewing with *Rs* almost straight; $2 + 3rm$ proximal to $2m\text{–}cu$; $1m\text{–}cu$ and Cu_{1a} basally separated. Hindwing with 14 hamuli on R_1; distal abscissa of Cu_1 present.

CI = 0·70–0·90*; BI = 1·20–1·30*; DBI = 0·50–0·60*; MI = 1·30–1·40*; RI = 1·40–1·45*; NI = 1·20*; PI = 2·20–2·40*.

Propodeum reticulate, spiracle at least 2·0 times as long as broad; apex of propodeum reaching about 0·3 of length of hind coxae; gaster elongate.

♂ genitalia. Single syntergum present; ninth abdominal sternite transverse, posteriorly truncate, centrally membranous (a unique feature); gonosquamae short. Gonolacinia distally evenly rounded about 45°; teeth moderate; apodeme straight, extending about 0·45 of length of basivolsellar strut. Distivolsella elongate, basally about 0·5 times as broad as long; clasping face rather flat, with a marked diagonal ridge bearing teeth. Paramere proximally slightly swollen, apically rounded. Aedeagus in profile angled, apically bilobate, dorsally concave; apicodorsal membranous area discrete, ventral membranous area present, the latter without spines, and laterally weakly extended; lateral sclerotized region of aedeagus reaching to the distal apex and apically bearing small spines (Text-figs 59, 83, 91, 115).

The features distinguishing *Clypeocampulum* from all described Palaearctic genera are the sculptured clypeus, indistinct occipital carina and single mid tibial spur. It is difficult to ascertain as to where this genus should most correctly be placed. The wing venation and general morphology show a similarity to *Barylypa*. However, the aedeagus is very unlike that of *Barylypa*, and more reminiscent of *Habronyx* (*Habrocampulum*). The lack of notauli, absence of a transverse furrow on the pronotum and position of Cu_{1a} in the forewing clearly exclude *C. tibiale* from *Habronyx*. It is suggested that for the purpose of cataloguing, *Clypeocampulum* should be included between *Aphanistes* and *Barylypa*.

Clypeocampulum is similar to *Liopterna* in venation and possession of a single mid tibial spur, but differs from this genus (as described by Townes, 1971) in the following ways:

—clypeus sculptured; that of *Liopterna* is not;
—occipital carina incomplete; that of *Liopterna* is complete;
—mesoscutum evenly rounded anteriorly; that of *Liopterna* is abruptly rounded;
—epicnemial carina reaching anterior margin of mesopleuron at level of posterior pronotal impression; that of *Liopterna* extends only just above level of lower corner of pronotum;
—tarsal claws small and basally pectinate; those of *Liopterna* are long, weakly curved and not pectinate (as both species are described from males, this may not be attributed to sexual dimorphism);
—posterior transverse carina of mesosternum narrowly interrupted before each mid coxa; that of *Liopterna* is absent except for a lateral vestige;
—mandible bidentate; that of *Liopterna* is unidentate.

Distribution. This genus is only recorded from Turkey.

Included species. Only the type-species is referable to this genus at present.

Clypeocampulum tibiale sp. n.

Holotype ♂, Turkey: Mugla, 40 kms, Fethiye-Ortaca road, 15.iv.1962 (*Guichard & Harvey*) (BMNH).

Forewing 7·5 mm.

Lower face flat, punctate; distance from orbit to anterior tentorial pit much less than distance from orbit to base of mandible; frons rugose, median vertical carina about 2·0 times as raised as broad, extending from just below median ocellus to between antennal bases. Flagellum with 31 segments. Head posteriorly neither buccate nor strongly narrowed.

Mesoscutum with weak transverse furrows before scuto-scutellar groove, centrally coarsely punctate, laterally finely punctate; scutellum convex, not carinate laterally.

Head black, inner margins of eyes broadly yellow; vertex with brown marks extending down the genae for 0·25 of their length; antennae brown, scape yellow-marked ventrally.

Thorax immaculately black; coxae black; forelegs yellowish, middle and hind legs brown; hind trochanter and trochantellus darker; all tibiae with a pronounced whitish pubescence.

Abdomen dark brown, apical segments entirely black; tergites 2 and 3 basally black; gonosquamae brown.

♀ unknown.

Paratype. TURKEY: 1 ♂, Adana, Ciftehan, 26.v.1960 (*Guichard & Harvey*) (BMNH).

Genus ***BARYLYPA*** Foerster

Barylypa Foerster, 1868 : 146. Type-species: *Anomalon genalis* Thomson, 1892 : 73, by subsequent designation (Viereck, 1914*a* : 19).

Laphyctes Foerster, 1868 : 146. Type-species: *Laphyctes insidiator* Foerster, 1878 : 73, by subsequent designation (Viereck, 1914 : 19). [Homonym of *Laphyctes* Dujardin, 1844.]

Sarntheina Dalla Torre, 1901 : 161. [Replacement name for *Laphyctes* Foerster.]

Hadromanus Szépligeti, 1905*a* : 14. Type-species: *Anomalon laevicoxis* Schmiedeknecht, 1900 : 241, by monotypy. **Syn. n.**

Magnibucca Morley, 1913*a* : 79. Type-species *Magnibucca testacea* Morley, 1913*a* : 80, by monotypy.

Trochiscomerus Meyer, 1931 : 8. Type-species: *Trochiscomerus schmiedeknechti* Meyer, 1931 : 9, by monotypy. **Syn. n.**

Eye without pubescence, inner margin at most weakly convergent ventrally; occipital carina complete, close to posterior ocelli; frons with a median vertical carina. Antennae short to moderately long, those of ♀ without a white band; scape truncate, about 1·2–1·5 times as long as pedicel; fourth flagellar segment about 2·5 times as long as broad. Clypeus with, rarely without, a median apical tooth; mandibles bidentate, apex not twisted, upper tooth distinctly the longer; labial palp with four segments; cardo basally lobed. Genal carina joining hypostomal carina at or immediately before the mandibular base.

Pronotum dorsally long, subhorizontal, without a transverse furrow (Text-fig. 207); posterior corner not covering spiracular sclerite; lower anterior margin of pronotum without a tooth, lower corner truncate. Anterior of mesoscutum abruptly rounded without an apical concavity; notauli weak or absent; medio-posterior region of mesoscutum punctate; transverse suture of mesoscutum absent, transverse impressed furrows absent. Epicnemial carina various, not medio-ventrally produced; sternaulus indistinct; posterior transverse carina of mesosternum interrupted in front of each mid coxa.

Fore coxae smooth; fore tibial spur with numerous acute macrotrichia along inner face. Mid tibia with two spurs. Hind trochanter more than 2·0 times as long as trochantellus; hind tarsi of ♂ not swollen; hind tarsal claws curved, basally pectinate, not obviously sexually dimorphic.

Forewing with *Rs* straight; 2 + 3*rm* proximal to 2*m–cu*; 1*m–cu* and Cu_{1a} basally separated. Hindwing with 10–15 hamuli on R_1; distal abscissa of Cu_1 present.

CI = 0·25–0·65; BI = 1·40–1·80; DBI = 0·40–0·60; MI = 1·30–1·70; RI = 1·00–2·30; NI = 0·70–3·10; ICI = 2·30+; PI = 3·50–4·00.

Propodeum reticulate, spiracle about 2·0 times as long as broad; apex of propodeum reaching about 0·5 of length of hind coxae. Gaster elongate.

♀ genitalia. Valvula 3 a little longer than apical abdominal depth; apex of ovipositor constricted, constricted part less than 3·0 times as long as median thickness of ovipositor; extreme apex weakly decurved with small lateral teeth; ovipositor not obviously laterally compressed (Text-fig. 19).

♂ genitalia. Single syntergum present; ninth abdominal sternite transverse, posteriorly truncate; gonosquamae short and obtuse. Gonolaciniae distally evenly rounded about 75°, teeth small; apodeme continuous, not angled, extending about 0·4 of length of basivolsellar strut. Distivolsella moderately broad, basally about 0·65 times as wide as long; clasping face flat with a weak transverse or diagonal ridge bearing teeth. Paramere proximally rounded. Aedeagus in profile fairly straight, apically truncate, dorsally flat; small apical membranous area present, remainder of aedeagus heavily and evenly sclerotized except for a long ventral spinose area, which is not laterally extended (Text-figs 64, 88, 118, 119).

Perkins (1962) pointed out that Viereck (1914) made an invalid selection of type for the genus *Erigorgus*; Brischke assigned three species definitely to *Erigorgus*, namely *Anomalon fibulator* Gravenhorst, *A. perspicillator* Gravenhorst and *A. rufum* Holmgren and also described *Anomalon* (?*Erigorgus*) *carinatum* as new. The selection of this species as type by Viereck was erroneous because a species doubtfully referred to a genus is not available for selection as the type-species. As a result of this invalid selection of type-species, Morley included *Barylypa* within *Erigorgus* (= *Anomalon* Jurine sensu authors). Perkins corrected this matter be selecting *Anomalon fibulator* Gravenhorst as the type-species of *Erigorgus* and placing *A. carinatum* within *Barylypa*.

Several species included by later authors within *Barylypa*, that is *B. uniguttata*, *B. humeralis*, *B. delictor* and *B. pallidens*, have been transferred to the genus *Hadromanus* by Townes (1971).

The distinction between *Barylypa* and *Hadromanus* is not particularly clear. The former is described as having the notauli present, but weak, reaching the centre of the mesoscutum or beyond, whereas *Hadromanus* species have no discernible notauli. However, there are in the collections of the BMNH a number of specimens of *B. carinata* (det. J. F. Perkins) which have no discernible notauli.

A further described difference between the two groups is the position of the epicnemial carina. *Barylypa* is described as having the epicnemial carina distant from the front edge of the mesopleuron and extending above the lower corner of the pronotum, whereas in *Hadromanus* the upper end of the epicnemial carina is angled to meet the front edge of the mesopleuron at the lower corner of the pronotum. There are specimens in both groups in which the epicnemial carina is short, not extending above level of lower corner of pronotum, and not angled at upper end.

It is apparently possible to distinguish between these two species-groups by examination of the wing venation (these hitherto overlooked characters were found to work for the twenty species examined). In *Hadromanus* BAI = 0·80–0·95 and NI = 1·25–3·10, but in *Barylypa* BAI = 1·05–1·15 and NI = 0·70–0·85.

In specimens referable to both groups there is some variation in the position of the petiolar spiracles, and in the position of the genal carina which makes generic separation using these characters unreliable.

The male genitalia of the two groups have been found to be very similar indeed and quite distinct from the remaining Therionine genera. Although some specific differences were observed it was not found to be possible to separate *Hadromanus* from *Barylypa* using features of the male genitalia.

In view of the close similarity between *Barylypa* and *Hadromanus*, it is suggested that the latter genus be included with *Barylypa* as formally stated above.

Townes (1971) included *Trochiscomeris schmiedeknechti* within *Hadromanus*. In this work the genus *Trochiscomeris* is treated as a synonym of *Barylypa*. However, it has not been possible to examine the holotype, and only specimen known, of *T. schmiedeknechti* as the specimen was destroyed. The description by Meyer (1931) indicates that his specimen may have been an exceptional one. It differed from the above generic diagnosis in having the 2 + 3*rm* vein distal to 2*m–cu* (the position of 2 + 3*rm* is a particularly variable feature) and having the hind tibia with a single spur. The author has not found any other Anomalonids with a single hind tibial spur but it has been noted that there is occasional reduction or even the atrophy of one mid tibial spur (this reduction is usually only found on one leg) and it is therefore possible that the specimen Meyer had before him was in fact a unique and malformed specimen. Unless further specimens are discovered *Trochiscomeris* is undoubtedly best included here.

Distribution. The species of this genus are most common in the southern Palaearctic region, but the genus is widely distributed throughout all regions except the Ethiopian.

Included species. The following species were examined:

B. elongata (Davis), *B. sulcata* (Provancher), *B. bipartita* (Morley), *B. xanthomelas* (Brullé), *B. apicate* (Cameron), *B. coarctata* Ashmead, *B. perturbans* Morley, *B. victoriana* Morley, *B. carinata* (Brischke), *B. delictor* (Thunberg), *B. humeralis* Brauns, *B. insidiator* Foerster, *B. rubricator* (Szépligeti), *B. rufa* (Holmgren), *B. uniguttata* (Gravenhorst), *B. longicornis* Brauns, *B. testacea* (Morley) and *B. frisiaca* Habermehl.

Three further undescribed species have also been examined.

Genus ***CORSONCUS*** Townes

Corsoncus Townes, 1971 : 141. Type-species: *Anomalon magum* Cresson, 1874 : 379, by original designation.

Eye without pubescence, inner margin weakly convergent ventrally; occipital carina usually completely absent on upper 0·5 of head, but strong and often raised into a flange latero-ventrally, rarely with medio-dorsal part only of occipital carina present on upper 0·5 of head; frons with a faint median vertical carina. Antennae moderately long, those of ♀ without a white band; scape truncate, 2·0 times as long as pedicel; fourth flagellar segment about 2·5 times as long as broad. Clypeus with median apical tooth; mandibles bidentate, lower tooth distinctly shorter than upper tooth, apices not twisted; labial palpi with four segments. Genal carina reaching base of mandible.

Pronotum dorsally long, subhorizontal, without or with very indistinct transverse furrow; posterior corner not covering spiracular sclerite; lower anterior margin of pronotum without a tooth, lower corner truncate. Anterior of mesoscutum abruptly rounded without an apical

concavity; notauli broad and shallow, extending beyond centre of mesoscutum; medio-posterior region of mesoscutum punctate; transverse suture of mesoscutum absent; transverse furrows absent. Epicnemial carina not reaching to centre of mesopleuron, close to anterior margin of pleuron, medio-ventrally rather strongly raised into a flange; sternaulus represented by a more coarsely punctate area; posterior transverse carina of mesosternum interrupted in front of each mid coxa.

Fore coxae smooth; fore tibial spur with numerous acute macrotrichia on inner face. Mid tibia with two spurs. Hind trochanter about 1·2 times as long as trochantellus; hind tarsi of ♂ not swollen; hind tarsal claws rather small, pectinate nearly to apex, not obviously sexually dimorphic.

Forewing with *Rs* almost straight; 2 + 3*rm* proximal to 2*m–cu*; 1*m–cu* and Cu_{1a} basally separated. Hindwing with 11–13 hamuli on R_1; distal abscissa of Cu_1 present.

CI = 0·30–0·40; BI = 1·20–1·35; DBI = 0·55–0·65; MI = 1·30–1·50; RI = 1·40–1·65; NI = 3·30–4·15; ICI = 2·10–2·30; PI = 2·70–5·00.

Propodeum reticulate, spiracle about 2·0 times as long as broad; apex of propodeum reaching about 0·6 of length of hind coxae. Gaster elongate.

♀ genitalia. Valvula 3 slightly longer than apical abdominal depth; apex of ovipositor constricted, constricted part about 3·0 times as long as median thickness of ovipositor; extreme apex a little decurved; ovipositor laterally compressed weakly.

♂ genitalia. Single syntergum present; ninth abdominal sternite transverse, posteriorly truncate; gonosquamae short and obtuse. Gonolaciniae distally evenly curved about 80°; teeth large; apodeme angled about 10° from axis, very short, not reaching 0·2 of length of basivolsellar strut. Distivolsella moderately broad, basally about 0·65 times as wide as long; clasping face weakly concave with transverse ridge bearing teeth. Aedeagal paramere proximally weakly spatulate, terminally rounded. Aedeagus in profile weakly sinuate, distal end expanded, apex abruptly rounded; small dorsal membrane extending distally and curved to form hook-shaped appendage; remainder of aedeagus weakly but evenly sclerotized, except for apicoventral region which is spinose and membranous.

Species of this genus are exceptional in having a lateral vertical keel immediately proximal to the anterior ventral membrane on the aedeagus (Text-figs 79, 85, 120).

Corsoncus species closely resemble *Barylypa*, especially *B. relictum* and *B. orbitale*. The distinguishing feature of *Corsoncus* is the form of the occipital carina. However, specimens of *B. relictum* and *B. orbitale* exist (in the collections of the BMNH) in which the occipital carina is absent laterally above the centre, though present centrally. This is very similar to an undescribed species of *Corsoncus* from Mexico (R. C. L. Perkins coll., BMNH). There is a second undescribed species from Vera Cruz (H. H. Swinnerton coll., BMNH) which has all the features of *Corsoncus* except that the occipital carina is present except centrally. The Vera Cruz specimen has, like *C. magus*, the epomia strongly divergent from the anterior margin of the pronotum but the Mexican species has the epomia less strongly divergent. The variation of these features suggest that it would perhaps be more consistent to include *Corsoncus* within *Barylypa*.

The form of the male genitalia of *Corsoncus* is particularly distinct from that of *Barylypa* in having a raised lateral keel. This unusual feature is also found in *B. relictum* and *B. orbitale*. This aedeagal keel is not found in other New World *Barylypa* species, as *B. anale* (Say) was found to have an aedeagus without a keel, and of the typical *Barylypa* form. This latter species also has the occipital carina complete. It is therefore apparent that *C. magus*, *B. relictus*, *B. orbitalis* and the undescribed *Corsoncus* species constitute a distinct species-group, and for

the present it is suggested that all species are included within *Corsoncus* as a distinct genus.

Corsoncus may be distinguished from *Barylypa* in having the occipital carina incomplete, usually centrally, but also sometimes laterally, and in having an aedeagus with a raised lateral keel. The status of *Corsoncus* needs further investigation.

Distribution. This genus is recorded only from the New World.

Included species. The following species were examined: *C. magus* (Cresson), *C. relictus* (F.) **comb. n.** and *C. orbitalis* (Cresson) **comb. n.** Two further undescribed species have been examined.

Genus ***LIOPTERNA*** Townes

Liopterna Townes, 1971 : 138. Type-species: *Liopterna schlingeri* Townes, 1971 : 138, by original designation.

Nothing at present can be added to the description included by Townes. This genus is known only from the holotype of the type-species, a male, which lacks the genital capsule.

Distribution. This genus is recorded only from California.

Genus ***PSEUDANOMALON*** Szépligeti

Pseudanomalon Szépligeti, 1905*a* : 33. Type-species: *Pseudanomalon gracile* Szépligeti, 1905*a* : 34, by monotypy.

Eye without pubescence, inner margin weakly convergent ventrally; occipital carina complete, close to posterior ocelli; frons without a median vertical carina. Antennae very long, those of ♀ without a white band; scape truncate, about 1·2 times as long as pedicel; fourth flagellar segment about 4·0 times as long as broad. Clypeus with a median apical tooth; mandibles bidentate, lower tooth obviously the shorter; labial palps with four segments, cardo basally lobate. Genal carina reaching base of mandible separate from hypostomal carina.

Pronotum dorsally narrow, subvertical, with a distinct transverse furrow which is centrally indiscernible; posterior corner completely covering spiracular sclerite; lower anterior margin of pronotum without a tooth, lower corner acute. Anterior of mesoscutum strongly but evenly rounded without an apical concavity; notauli distinct to hind margin of mesoscutum; medio-posterior region of mesoscutum rugose; transverse suture of mesoscutum absent, transverse furrows absent. Epicnemial carina distinct, reaching 0·4 of way up mesopleuron, apically angled to reach anterior margin of pleuron, medio-ventrally not produced; sternaulus discernible as a broad shallow groove; posterior transverse carina of mesosternum complete.

Fore coxae smooth; fore tibial spur with numerous macrotrichia on inner surface. Mid tibia with two spurs. Hind trochanter about 2·5 times as long as hind trochantellus; hind tarsi of ♂ not swollen; hind tarsal claws curved, pectinate to apices, not obviously sexually dimorphic.

Forewing with *Rs* almost straight; 2 + 3*rm* distal to *2m–cu*; 1*m–cu* and Cu_{1a} basally separated. Hindwing with 9–11 hamuli on R_1; distal abscissa of Cu_1 present.

CI = 1·20–1·40*; BI = 1·40–1·55*; DBI = 0·65–0·75*; MI = 2·30–2·70*; RI = 2·00–3·05*; NI = 3·00+*; ICI = 2·20+*; PI = 3·90–4·30*.

Propodeum reticulate, spiracle about 1·5 times as long as broad; apex of propodeum reaching about 0·4 of length of hind coxae. Gaster elongate.

♀ genitalia. Valvula 3 a little longer than apical abdominal depth; apex of ovipositor evenly

elongately acute; extreme apex not decurved; ovipositor weakly laterally compressed (Text-figs 6, 14, 28).

♂ genitalia. Single syntergum present; ninth abdominal sternite very transverse, posteriorly truncate; gonosquamae short, acute. Gonolacinia distally abruptly angled about 85°; teeth small but numerous; apodeme angled about 5° to axis, extending about 0·5 of length of basivolsellar strut. Distivolsella moderately broad, basally about 0·65 times as wide as long; clasping face concave, with small ridge bearing teeth. Paramere proximally bluntly rounded. Aedeagus in profile swollen, apically rounded, dorsally convex; narrow apical membranous area present, but remainder of aedeagus rather evenly sclerotized; ergots particularly obvious (Text-figs 40, 77, 117).

This is a particularly distinctive genus. The species are apparently modified for nocturnal existence as they exhibit a pronounced 'Ophionoid facies' (Gauld & Huddleston, in press). This genus does not appear to be particularly closely related to any other described genus.

Distribution. Widely distributed throughout the Old World Tropics from central and western Ethiopian regions, to New Guinea and New Hebrides.

Species of this genus appear to be rather rare.

Included species. The following species have been examined:
P. gracile Szépligeti, *P. rectum* Morley and three further undescribed species.

Genus ***THERION*** Curtis

Therion Curtis, 1829 30 : 101. Type-species: *Ichneumon circumflexus* Linnaeus, 1758 : 566, by original designation.

Therium Agassiz, 1846 : 368. [Unjustified emendation.]

Exochilum Wesmael, 1849 : 119, 122. Type-species: *Ichneumon circumflexus* Linnaeus, 1758 : 566, by monotypy.

Eye without pubescence, inner margins ventrally parallel; occipital carina complete, close to posterior ocelli; frons with a median vertical carina or a lamella, or a cornute process, the protruberance not reaching down between antennal bases. Antennae short to moderately long, those of ♀ without a white band; scape truncate, about 1·6 times as long as pedicel; fourth flagellar segment about 1·2 times as long as broad. Clypeus apically truncate; mandible bidentate, apically not twisted, lower tooth a little shorter than upper; labial palp with four segments; cardo basally lobate. Genal carina joining base of mandible.

Pronotum dorsally rather narrow, subvertical, with a transverse impressed furrow; posterior corner not covering spiracular sclerite; lower anterior margin of pronotum with or without a tooth, lower corner acute. Anterior of mesoscutum rather evenly rounded, with a weak apical concavity; notauli weak; medio-posterior region of mesoscutum coarsely punctate; transverse suture of mesoscutum absent, transverse furrows absent. Epicnemial carina reaching above centre of mesopleuron, its upper end reaching anterior margin of pleuron, medioventrally not produced into a flange; sternaulus very broad and shallow; posterior transverse carina of mesosternum interrupted in front of each mid coxa.

Fore coxae smooth; fore tibial spur with numerous sub-acuminate macrotrichia along inner face. Mid tibia with two spurs; hind trochantellus and trochanter approximately equal in length; hind tarsi of ♂ swollen, ventral surface of second and third tarsal segments flattened, with a median longitudinal carina, more or less glabrous; hind tarsal claws curved, pectinate basally, not obviously sexually dimorphic.

Forewing with *Rs* almost straight; 2 + 3*rm* proximal to 2*m–cu*; 1*m–cu* and Cu_{1a} basally separated. Hindwing with 11–17 hamuli on R_1; distal abscissa of Cu_1 present.

CI = 0·95–1·40; BI = 2·00–3·00; DBI = 0·95–1·10; MI = 1·45–1·75; RI = 2·10–2·75; NI = 0·45–0·95; ICI = 1·10–1·50; PI = 3·00–3·65.

Propodeum reticulate, spiracles about 2·5 times as long as broad; apex of propodeum reaching 0·6 of length of hind coxae. Gaster elongate.

♀ genitalia. Valvula 3 about as long as apical depth of abdomen; apex of ovipositor somewhat constricted, long, slender and acute; extreme apex decurved; ovipositor not laterally compressed; rather heavily sclerotized nodus present dorsally (Text-figs 10, 24).

♂ genitalia. Usually with a single syntergum present; ninth abdominal sternite transverse to rather cubical, posterior margin bowed or rounded; gonosquamae short, variable. Gonolacinia distally abruptly and angularly rounded about 90°; teeth well developed; apodeme angled about 40° from axis of gonolacinia, short, not extending 0·25 of length of basivolsella strut. Distivolsella slender, basally less than 0·5 times as wide as long, distally a little swollen; teeth arranged diagonally across the clasping face. Paramere proximally rounded. Aedeagus in profile geniculate, apically truncate, evenly sclerotized except for membranous areas; apicolateral region of aedeagus with a row of large spines; distal end of lateral sclerotized region angled ventrally, reaching margin of aedeagus and extreme distal end bearing spines; ventral region not laterally extended (Text-figs 38, 57, 69, 123).

Undoubtedly the 'Theriine' genera (that is *Therion*, *Heteropelma* and *Tanypelma*) share a number of common characters, but there is some overlap with other genera. *Therion* is quite distinct from the other two genera in many features, notably the shape of the tarsal claws, shape of the lower face and form of the male genitalia.

The characters that have been used for separating the 'Theriine' genera from the 'Gravenhorstiine' genera are the presence of pronotal tooth, value of DBI, and shape of clypeus. The variation of the values of DBI have already been referred to. The tooth characteristically present on the lower anterior margin of the pronotum in the 'Theriine' genera has been found to be vestigial or absent in many specimens of *Therion* (Text-fig. 202). In *Habronyx* (*Habrocampulum*) *biguttatum*, the pronotal tooth is present (Text-fig. 201) although this species is in other ways typically 'Gravenhorstiine'. It is apparent that the presence of this tooth is not a stable enough character to permit reliable distinction between the 'Theriine' and 'Gravenhorstiine' groups. Some species of *Barylypa* resemble *Therion* in having the clypeus truncate, so therefore the form of the clypeus alone will not allow the distinction of the two groups.

Short (1959) found characters to permit separation of 'Theriine' and 'Gravenhorstiine' final instar larvae, but the larvae of *Trichomma* are intermediate between those of the two groups, and the larvae of *Encardia* are far more similar to those of the 'Theriine' genera, than to the genera to which *Encardia* is presumed closely related.

It is suggested that, whilst accepting the 'Theriine' genera (excluding *Brachynervus*) form a somewhat distinct group, according this group higher taxonomic status than that of a genus-group is not in keeping with the classification of the subfamily as a whole and should not be employed.

The relationships of *Therion* with other genera is not resolved at present. However, a particular combination of features found in *Therion* species has also been observed in other genera. The swollen distivolsella, the broad epistomal arch of the larva, and the 'Aladdin's lamp' egg are features shared by *Therion*, *Heteropelma* and *Tanypelma* (Text-figs 96–98). These features are also found in *Trichomma*

(though in a rather modified form) and also in *Habronyx* (*Habronyx*) and to a lesser extent in *H.* (*Camposcopus*). As far as is known none of the other genera share this combination of features. It is suggested, therefore, that the 'Theriine' genera are related to *Habronyx*, and to *Trichomma* (which is evidently a rather specialized genus) less closely.

Distribution. This is predominantly a Holarctic genus with some species extending to central America and south-east Asia.

Included species. The following species have been examined:

T. circumflexum (L.), *T. brevicorne* (Gravenhorst), *T. nigripes* Dreisbach, *T. fuscipenne* (Norton), *T. texanum* (Ashmead), *T. nox* (Morley), *T. morio* (F.), *T. mussouriense* (Cameron), *T. giganteum* (Gravenhorst), *T. neglectum* (Morley), *T. tenuipes* (Norton) and *T. ericae* Bauer.

Genus *HETEROPELMA* Wesmael

Heteropelma Wesmael, 1849 : 120. Type-species: *Heteropelma calcator* Wesmael, 1849 : 120, by monotypy.

Schizoloma Wesmael, 1849 : 120. Type-species: *Ichneumon amictus* (F.), 1775 : 341, by monotypy.

Schizopoma Foerster, 1868 : 145, 220. [Unjustified emendation.]

Eyes without pubescence, inner margins convergent ventrally; occipital carina varying in position from close to posterior ocelli to very widely separated from posterior ocelli; frons with a median vertical carina and a lamella between bases of antennae. Antennae long, those of ♀ without a white band; scape truncate, about 1·6 times as long as pedicel; fourth flagellar segment about 2·0 times as long as broad. Clypeus truncate with or without lateral corners reflexed; mandible bidentate, lower tooth obviously the shorter; labial palps with four segments; cardo basally lobed. Genal carina reaching base of mandible.

Pronotum dorsally long, subvertical, without a transverse impressed furrow; posterior corner partially occluding spiracular sclerite; lower anterior margin of pronotum with a large tooth, lower corner acute. Anterior of mesoscutum abruptly but not irregularly rounded, without an apical concavity; notauli very weak to moderately strongly impressed; medio-posterior region of mesoscutum coriaceous or coarsely punctate; transverse suture of mesoscutum absent, transverse furrows absent. Epicnemial carina usually reaching above centre of mesopleuron, its upper end reaching anterior margin of pleuron, medio-ventrally not raised into flange; sternaulus indistinct; posterior transverse carina of mesosternum complete, not at all interrupted.

Fore coxae smooth; fore tibial spur with numerous acute macrotrichia along inner face. Mid tibia with two apical spurs, rarely with reduction of the inner spur so superficially appearing unicalcarate. Hind trochanter a little longer than, equal to, or a little shorter than, the trochantellus; ♂ hind tarsi swollen, second segment usually with an elongate sunken area which bears flattened macrotrichia, if rarely without sunken area then flattened macrotrichia are still present on ventral tarsal surface; hind tarsal claws geniculate, basally lobate, except in one Australian species in which the claws are simply curved; claws not obviously sexually dimorphic.

Forewing with *Rs* weakly sinuate; 2 + 3*rm* proximal to 2*m-cu*; 1*m-cu* and Cu_{1a} basally separate. Hindwing with 12–16 hamuli on vein R_1; distal abscissa of Cu_1 present.

CI = 0·65–1·00; BI = 1·70–1·90; DBI = 0·80–1·05; MI = 1·70–1·95; RI = 1·40–1·70; NI = 0·30–0·55; ICI = 0·60–1·20; PI = 2·20–2·90.

Propodeum reticulate, spiracle about 2·5 times as long as broad; apex of propodeum reaching about 0·5 of length of hind coxae. Gaster elongate.

♀ genitalia. Valvula 3 a little longer than apical depth of abdomen; apex of ovipositor elongately constricted, acutely pointed; extreme apex decurved; ovipositor not at all laterally compressed; heavily sclerotized nodus present dorsally (Text-figs 2, 3, 18).

♂ genitalia. Single syntergum present; ninth abdominal sternite almost quadrate, posteriorly rounded; gonosquamae short, usually acute apically. Gonolaciniae distally abruptly angled about 90°; teeth small; apodeme angled about 20° from axis of gonolacinia, long, reaching 0·75 of length of basivolsellar strut. Distivolsella slender, basally less than 0·5 times as wide as long, distally swollen; teeth arranged diagonally across clasping face. Paramere proximally rounded. Aedeagus in profile sinuate, apically weakly bilobate, rather evenly sclerotized but with a more membranous ventral region bearing a few scattered spines on extreme ventral margin; distal end of lateral sclerotized region reaching apex of aedeagus; ventral region not laterally extended (Text-figs 30–33, 52, 70, 122).

A particularly distinctive feature of this genus is the possession by males of flattened hairs on the ventral surface of the second hind tarsus. The function of these presumably sensory appendages is unknown, but the hind legs are used to attract females. The males of this genus display, adopting a very characteristic flight pattern with the hind legs broadly out-stretched so that the explanate and and usually brightly coloured hind tarsi are particularly obvious.

Heteropelma is one of the most easily recognizable genera, but even so, there is some variation of characters previously considered diagnostic of this genus. *H. perornatum* is distinct from other species in having the head strongly narrowed behind the eyes (Text-figs 175, 176) and often the inner mid tibial spur is reduced so that it superficially appears that the tibia is unicalcarate. The shape of the hind tarsal claws has been used by some workers as a diagnostic feature of this genus and indeed the majority of species have the typical strongly geniculate claws. One species, *H. flavitarse*, is characterized by having simply curved hind tarsal claws (Gauld, 1974).

Distribution. This genus has been recorded from all regions except the Neotropical, Nearctic and Ethiopian.

In many areas species of this genus are the most common Anomaloninae observed.

Included species. The following species have been examined:

H. calcator Wesmael, *H. amictum* (F.), *H. acheron* (Morley), *H. elongatum* Uchida, *H. capitatum* (Desvignes), *H. flavitarse* (Brullé), *H. fulvitarse* Cameron, *H. perlongum* Cushman, *H. perniciosum* (Turner), *H. perornatum* (Cameron), *H. reticulatum* Cameron, *H. scaposum* (Morley), *H. fulvicorne* (Cameron) and *H. tinctipenne* (Cameron).

Genus ***TANYPELMA*** Townes

Tanypelma Townes, 1971 : 157. Type-species: *Heteropelma fulvicorne* Townes, 1945 : 729, by original designation.

The name *Tanypelma* attributed by Brischke to Foerster appears as a synonym of *Orthopelma* Taschenberg (Brischke, 1881). There is no evidence that *Tanypelma* Foerster was ever published by Foerster. According to the *International Code of Zoological Nomenclature* names published before 1931 must be accompanied by a description, definition or indication (Article 12) and citation of a name in synonymy does not constitute an indication (Articles 16b; 11d). *Tanypelma* Foerster, Brischke

must therefore be disregarded and cannot be cited as a senior homonym of *Tanypelma* Townes.

Eyes without pubescence, inner margins almost parallel sided; occipital carina complete, separated from posterior ocelli by more than 2·0 times ocellar diameter; frons concave without a median vertical carina, lower part of frons with a lamella between antennal bases. Antennae moderately long, those of ♀ without a white band; scape truncate, 1·4 times as long as pedicel; fourth flagellar segment about 1·5 times as long as broad. Clypeus apically convex, without a medio-ventral tooth; mandibles bidentate, lower tooth a little shorter than upper, apices not twisted; labial palpi with four segments; cardo basally lobate. Genal carina reaching base of mandible, remote from hypostomal carina.

Pronotum dorsally long, subvertical, with a broad weak transverse impressed furrow; posterior corner not occluding spiracular sclerite; lower anterior margin of pronotum with a large tooth, lower corner acute to rounded. Anterior of mesoscutum abruptly but not irregularly rounded, without an apical concavity; notauli weak but discernible, extending to centre of mesoscutum; medio-posterior region of mesoscutum coarsely punctate; transverse suture of mesoscutum absent, transverse furrows absent. Epicnemial carina usually reaching above centre of mesopleuron, inclined towards the anterior margin of the pleuron, medio-ventrally not produced into a flange; sternaulus indistinct; posterior transverse carina of the mesosternum complete, not at all interrupted.

Fore coxae smooth, fore tibial spur with numerous acute macrotrichia along inner face. Mid tibia with two apical spurs. Hind trochanter about equal in length to the trochantellus; ♂ hind tarsi not swollen; hind tarsal claws geniculate, basally lobate, not obviously sexually dimorphic.

Forewing with *Rs* weakly sinuate; $2 + 3rm$ proximal to $2m\text{-}cu$; $1m\text{-}cu$ and Cu_{1a} basally separate. Hindwing with 14–18 hamuli on vein R_1; distal abscissa of Cu_1 present.

Cl = 0·95–1·05*; BI = 1·80–2·15*; DBI = 0·85–1·00*; MI = 1·50–1·70*; RI = 1·50–1·60*; NI = 0·80–0·90*; ICI = 2·10–2·30*; PI = 1·90–2·20*.

Propodeum reticulate, spiracle about 3·5 times as long as broad; apex of propodeum reaching about 0·5 of length of hind coxae. Gaster elongate.

♀ genitalia. Valvula 3 a little longer than apical depth of abdomen; apex of ovipositor constricted; extreme apex shortly acute, not obviously decurved; ovipositor dorsally flattened; heavily sclerotized nodus present dorsally.

♂ genitalia. Single syntergum present; ninth abdominal sternite transverse, posteriorly rounded with a small median impression; gonosquamae rather elongately pointed. Gonolaciniae distally abruptly angled about 90°; teeth reduced to ridge-like projections; apodeme angled about 20° from axis of gonolacinia, long, reaching 0·7 of length of basivolsellar strut. Distivolsella slender, basally about 0·5 times as wide as long, distally weakly swollen, clasping face concave with vertical median ridge weakly sloping away either side, with ventral side covered with teeth. Paramere proximally rounded. Aedeagus in profile sinuate, apically weakly bilobate, very evenly sclerotized, ventrally not laterally extended (Text-figs 55, 75, 121).

This genus is very closely related to *Heteropelma*, from which it differs, in addition to the characters mentioned above, in having the scutellum strongly swollen (that of *Heteropelma* is flat or centrally concave).

Distribution. This genus is restricted to the Nearctic region.

Included species. The following species have been examined:
T. fulvicorne Townes and *T. datanae* (Riley).

Genus ***ENCARDIA*** Tosquinet

Encardia Tosquinet, 1896 : 264. Type-species: *Encardia picta* Tosquinet, 1896 : 264, by monotypy.

Herus Tosquinet, 1903 : 394. Type-species: *Herus sagus* Tosquinet, 1903 : 395 [= *Encardia picta* Tosquinet, 1896 : 264], by monotypy. [Homonym of *Herus* Rehn, 1900.]
Ctenotoma Cameron, 1906 : 127. Type-species: *Ctenotoma fuscipennis* Cameron, 1906 : 128 [= *Encardia picta* Tosquinet, 1896 : 264], by subsequent designation (Viereck, 1914*a* : 39).
Ctenocaloides Fahringer, 1936 : 582. Type-species: *Ctenocaloides anareolatus* Fahringer, 1936 : 582 [= *Encardia picta* Tosquinet, 1896 : 264], by original designation.

Eyes with surface bearing hair, inner margins weakly convergent; occipital carina complete or centrally narrowly interrupted, separated from posterior ocelli by more than 2·0 times ocellar diameter; frons with a median vertical carina. Antennae moderately long, those of ♀ without a white band; scape almost truncate, about 1·3 times as long as pedicel; fourth flagellar segment about 1·5 times as long as broad. Clypeus with apex acute, with a median tooth; mandible bidentate, with wide flange on lower margin, lower tooth about as long as or even slightly longer than upper, not twisted appreciably; mouthparts unusual in being very reduced, labial palps with two segments, maxillary palps (in other genera the maxillary palps are 5-segmented) reduced to a finger-like appendage of one or two segments, if two, then division is not particularly clear; cardo with very weak lobes, membranous. Genal carina joining base of mandible separate from hypostomal carina.

Pronotum dorsally long, subhorizontal, with a broad transverse groove; posterior corner occluding upper 0·2 of spiracular sclerite; lower anterior margin without a tooth, lower corner rounded. Anterior of mesoscutum very evenly rounded, without an apical concavity; notauli present, weakly to strongly impressed to centre of mesoscutum; medio-posterior region of mesoscutum punctate; transverse suture of mesoscutum absent, transverse furrows absent. Epicnemial carina indistinct, when present extending only to level of lower corner of pronotum, medio-ventrally not raised into flange; sternaulus absent; posterior transverse carina of mesosternum usually completely absent.

Fore coxae smooth; fore tibial spur with numerous acute macrotrichia on inner face. Mid tibia with two spurs. Hind trochanter about 1·6 times as long as trochantellus, or longer; hind tarsi of ♂ not swollen; hind tarsal claws rather geniculate, not obviously sexually dimorphic.

Forewing with *Rs* almost straight; 2 + 3*rm* slightly proximal to 2*m–cu*; 1*m–cu* and Cu_{1a} basally separate. Hindwing with 10–13 hamuli on vein R_1; distal abscissa of Cu_1 present.

CI = 2·20–2·40; BI = 1·45–1·65; DBI = 0·50–0·64; MI = 1·60–1·90; RI = 2·05–2·37; NI = 1·22–1·43; ICI = 1·90–2·42; PI = 1·70–1·80.

Propodeum anteriorly smooth, posteriorly reticulate, spiracle about 2·5 times as long as broad; apex of propodeum not extended beyond 0·3 of length of hind coxae. Gaster short, not or weakly laterally compressed (the gaster of all other genera is laterally compressed); petiole unusual in being very short with inter-spiracular distance about 0·4 times as long as length of tergite (in most other genera inter-spiracular distance is less than 0·2 of length of tergite).

♀ genitalia. Valvula 3 a little longer than apical abdominal depth; apex of ovipositor abruptly constricted, constricted part about 2·0 times as long as median thickness of rather stout ovipositor, extreme apex weakly decurved, ovipositor not laterally compressed.

♂ genitalia. Syntergites separate; ninth abdominal sternite transverse, posteriorly truncate, very weakly sclerotized; gonosquamae short, truncate. Gonolaciniae distally weakly angled about 30°; teeth large, auxillary teeth present on inner surface; apodeme straight, extending about 0·2 of length of basivolsellar strut. Distivolsella moderately broad, basally about 0·6 times as wide as long; clasping face flat, spines scattered diagonally. Aedeagus in profile apically truncate, medianly strongly geniculate, swollen. Apex evenly sclerotized, except for a laterally weakly extended ventral membranous region (Text-fig. 116).

The shape of the gaster and the coloration make this genus one of the most distinctive amongst the Therionini.

In the collections of the BMNH are two specimens of *E. picta* together with the

Saturniid pupae from which they have emerged. Dissection of these have enabled the structure of the first instar larva and the head capsule of a final instar larva to be examined. One puparium was unusual in containing both the cast skin of a first instar larva and a dehydrated corpse of a second instar larva, showing that oviposition may have occurred twice in the same saturniid larva. Although the entire contents of the puparium had been consumed by the mature *Encardia* larva, it did not eat the other first instar *Encardia* larva.

The structure of the first instar larva is shown in Text-figs 153, 154. No sclerotized cephalic capsule was found to be present. The mandibles were observed to be minute, inserted apically on a stomal papillus. The mandibles were observed to have a pair of obvious spherical condyles which provided points of articulation. The size and positioning of the mandibles would seem to indicate that they are virtually non-functional. The most obvious feature of the larvae is the possession of an elongate caudal appendage. Similar appendages have been observed on the larvae of other species of Therionini, notably *Heteropelma calcator* (Plotnikov, 1914) and *Therion morio* (F.) (Tothill, 1922).

The cephalic capsule of the final instar larva of *E. picta* (Text-fig. 155) is more similar to that of *Heteropelma* species than to any other described species. *Encardia* differs from *Heteropelma* in the arrangement of the labral sensillae. Those of the latter are clustered into two separate groups, whereas those of the former are arranged in a single longitudinal group.

Distribution. Only recorded from Ethiopian region.

Included species. *Encardia* is a small genus which includes only the two species *E. picta* Tosquinet and *E. rufantennata* Benoit, which were examined.

Variation of these species has recently been discussed by Huddleston (1975).

Genus *GRAVENHORSTIA* Boie

Gravenhorstia Boie, 1836 : 42.

Eye with or without short pubescence, margins ventrally, at most rather weakly convergent; occipital carina complete, close to posterior ocelli; frons with at most an indistinct median vertical carina. Antennae short to moderately long, those of ♀ without a white band; scape truncate, always longer than pedicel (at least 1·5 usually more than 1·8 of length of pedicel); fourth flagellar segment about 1·4 times as long as broad. Clypeus apically convex to centrally pointed, with or without a median tooth; mandibles bidentate, rarely with a basal lobe, varying from equally bidentate to having lower tooth mutic, apices not or weakly twisted; labial palpi with four segments; cardo with weak lobes. Genal carina usually reaching base of mandible separate from rarely contiguous with hypostomal carina.

Pronotum dorsally long, subhorizontal, with a transverse furrow; posterior corner flat, not covering spiracular sclerite; lower anterior margin of pronotum without a tooth, lower corner acute or rounded. Anterior of mesoscutum smoothly and evenly rounded, apical concavity absent; notauli completely absent; medio-posterior region of mesoscutum punctate; transverse suture of mesoscutum absent, transverse furrows absent. Epicnemial carina usually short, not extending above lower 0·3 of mesopleuron and with upper end distant from the anterior margin of the mesopleuron, medio-ventrally not produced into a flange; sternaulus indistinct; posterior transverse carina of mesosternum interrupted before each mid coxa.

Fore coxae smooth; fore tibial spur with numerous acute macrotrichia along inner face. Mid tibia with two apical spurs. Hind trochanter less than 1·5 times as long as trochantellus;

hind tarsi of ♂ not explanate; hind tarsal claws very variable in shape, from long and simple to short and pectinate on basal half; those of ♀ always more extensively pectinate, usually though not always shorter and less strongly curved than those of ♂ (Text-figs 215–218).

Forewing with *Rs* sinuate; 2 + 3*rm* distal, opposite or proximal to *2m–cu*; 1*m–cu* and Cu_{1a} basally separated. Hindwing with 10–17 hamuli on R_1; distal abscissa of Cu_1 present.

Propodeum reticulate, spiracles more than 1·5 times as long as broad; apex of propodeum at most reaching 0·5 of length of hind coxa. Gaster compact to elongate (PI = 2·20–3·70).

♀ genitalia. Valvula 3 slightly longer than apical abdominal depth; apex of ovipositor constricted, constricted part at least 4·0 times as long as median thickness of ovipositor; extreme apex decurved; ovipositor not obviously laterally compressed (Text-fig. 23).

♂ genitalia. Single syntergum present; ninth abdominal sternite transverse; gonosquamae short, usually truncate. Gonolacinia distally evenly curved about 50°; teeth small to moderate; apodeme straight, extending about 0·4 of length of basivolsellar strut. Distivolsellar moderately to very broad, basally 1·00 times as wide as long; clasping face particularly flat, with a weak peripheral ridge bearing a few teeth (Text-figs 80, 108–111).

For the present this genus is restricted to those Therionini in which the mesoscutum is anteriorly smooth and evenly rounded in profile (Text-figs 204, 209), the claws are strongly sexually dimorphic, those of the male being long and weakly curved whilst those of the female are shorter and more strongly curved (Text-figs 215–218), the notauli entirely absent and the aedeagus apico-ventrally impressed (Text-figs 108–111). This therefore excludes a number of Australian species which, though quite closely related to *Gravenhorstia*, have the mesoscutum anteriorly more abruptly rounded and with impressed notauli. These species have been placed in *Habronyx* (*Australomalon*).

There has probably been more disagreement about the limits of this genus than about any other in the subfamily. Townes *et al.* (1965) included *Erigorgus* within *Gravenhorstia*, but in later work Townes (1971) treated these as distinct genera. Viktorov (1968) considered that *Gravenhorstia*, together with *Nenethes* and *Aubertia*, should be accorded the status of a separate subtribe, the Gravenhorstiina, as distinct from the Erigorgina. The diagnostic feature of the Gravenhorstiina was considered to be the form of the gaster, notably the fact that the second tergite is subequal to the length of the third. Because of the difference in shape of the gaster basally, Foerster (1868) considered that *G. picta* had more affinity with the Porizontini (Campoplegoidea, in part, sensu Foerster) although in all other features *G. picta* is typically Therionine. A variation in the lengths of the basal segments of the gaster of insects of one subtribe is an occurrence not unknown amongst other groups of Ichneumonids. For example, in the Cremastinae, *Eutanygaster* Cameron and *Eiphosoma* Cresson have the anterior abdominal segments far more elongate than those of the related genus *Cremastus* Gravenhorst. It is therefore considered that it is not justifiable to place *Gravenhorstia*, *Nenethes* and *Aubertia* in a separate subtribe.

Examination of a number of species has shown that there is an almost continuous range of variation in the form of the abdomen (Table 2). It can clearly be seen that there is a tendency towards elongation of the basal abdominal segments from *G. picta* to *G. cerinops*.

Examination of the genitalia of the species of *Gravenhorstia* reveals that there are definite affinities between the species (Text-figs 108–111). The extent of the

TABLE 2

Comparison of the subgenera of *Gravenhorstia*

GRAVENHORSTIA (*GRAVENHORSTIA*)	*GRAVENHORSTIA* (*KOKUJEWIELLA*)	*GRAVENHORSTIA* (*ERIGORGUS*)	*GRAVENHORSTIA* (*RIBASIA*)
Mandible basally simple; teeth subequal in length.	Mandible basally simple; teeth subequal to lower tooth distinctly the shorter.	Mandible basally simple; lower tooth distinctly the shorter, rarely almost absent.	Mandible basally lobate; lower tooth distinctly the shorter.
Clypeus apically rounded with small median tooth.	Clypeus apically rounded with small median tooth.	Clypeus apically pointed, usually with large median apical tooth.	Clypeus apically angularly rounded with blunt median apical tooth.
Scutellum convex.	Scutellum moderately convex.	Scutellum weakly convex to flat.	Scutellum convex.
Gaster short: LAI = 1·4–1·8, DAI = 1·1–1·3.	Gaster moderately long: LAI = 2·2–2·4, DAI = 1·2–1·4.	Gaster elongate: LAI = 2·6–4·6, DAI = 1·4–1·8.	Gaster moderately long: LAI = 3·0, DAI = 1·3.
Lower face with central cornute process, finely punctate.	Lower face without cornute process, finely punctate.	Lower face without cornute process, finely to coarsely punctate.	Lower face flat, coarsely and sparsely punctate.
Aedeagus with two lobules near apico-ventral impression; ventral membranous area with isolated spinules.	Aedeagus with a single lobule near apico-ventral impression; ventral membranous area with scattered spinules.	Aedeagus without lobes near apico-ventral impression; ventral membranous area moderately spinose.	Unknown.

apico-dorsal extension increases from *G. picta* to species traditionally placed within *Erigorgus*. In *G. picta* there are two processes at the anterior and ventral corners of the apicoventral impression and the ventral membranous area is evenly tapered. In *G. iberus* there is a single process on the ventral corner of the apicoventral impression and the ventral membranous area is short and broad. In species traditionally placed within *Erigorgus* there are no processes present.

There is an extraordinary degree of variation in the shape of the mandibles within this genus. In *G. picta* the mandibles are almost equally bidentate, in *G. ibera* the mandibular teeth are subequal, in *G. vicaria* the mandible is narrowed and with a basal flange, and in species traditionally placed within *Erigorgus*, the lower mandibular tooth is much smaller than the upper. In some undescribed species the lower mandibular tooth is almost entirely absent. In *G. erythrogaster* the mandible bears a large and singularly characteristic basal lobe (Text-fig. 157).

The larvae of this genus were examined by Beirne (1941) but no illustration or description of the cephalic capsule of the final instar larva is available. These structures have been examined for a number of species traditionally referable to *Erigorgus*. The cephalic capsules of all species examined were found to be similar to *Aphanistes* but without the posterior ends of the hypostomae extending to a point. In at least some species a minute vestige of the hypostomal spur was observed to be present (Text-fig. 147).

It can be seen from Table 2 that *Gravenhorstia* can be subdivided into four species-groups. It is suggested that these species-groups be treated as subgenera within the genus *Gravenhorstia*.

Subgenus ***GRAVENHORSTIA*** Boie

Gravenhorstia Boie, 1836 : 42. Type-species: *Gravenhorstia picta* Boie, 1836 : 43, by monotypy.
Odontopsis Foerster, 1868 : 150. Type-species: *Gravenhorstia picta* Boie, 1836 : 43 (included by Dalla Torre, 1901 : 200), by subsequent monotypy.

Surface of eye glabrous; lower face with a prominent median tubercle. Clypeus rounded with a median apical tooth; mandible equally bidentate, without a basal flange. Genal carina reaching base of mandible separate from hypostomal carina.

Mesoscutum evenly rounded, without any trace of notauli; scutellum strongly convex. Epicnemial carina indistinct, reaching to about the centre of the mesopleuron, its upper end widely separated from the anterior margin of the mesopleuron. Propodeum short, posteriorly extended about 0·45 of length of hind coxae.

Foreleg with basitarsus of ♂ at least 2·0 times as long as fifth tarsal segment; first subdiscal cell explanate; 14–17 hamuli on vein R_1; 2 + 3*rm* proximal, opposite or distal to 2*m–cu*.

CI = 1·10–1·65; BI = 1·75–2·10; DBI = 0·55–0·65; MI = 1·80–2·00; RI = 1·25–1·75; NI = 0·85–1·05; ICI = 1·40+.

♂ genitalia. Aedeagus in profile medianly angled, apicodorsally with a lobe, dorsally concave; apicodorsal lobe dorsally membranous, membrane extended proximally to angulation, and with a small ventrally directed membranous lobule; ventral membranous area discrete, bearing few spinules, produced apically into small upturned prominence, not laterally extended (Text-fig. 111).

Previous workers have often regarded this as a primitive species-group on account

of the form of the gaster. The present author regards this as a more evolved, specialized insect than *G.* (*Erigorgus*) *cerinops*. Evidence for this suggestion has been obtained from dissection of the female. The ovipositor is terminally markedly constricted, a feature presumably evolved to facilitate oviposition into early instar host larvae, but unlike other Therionini which have a very small egg (0·4 mm or less in length, even for a large species) *G. picta* has large eggs (0·8 mm or more). Although nothing is known about the biology of these insects, the size of the egg would seem to indicate that the insect oviposits in later instar larvae and, because of the form of the ovipositor, it is conceivable that this is a secondary reversion to a more usual habit and not a primary adaptation. It may well be that increase in depth and decrease in length of the basal segments of the gaster may be an adaptation to enclose the relatively larger muscles needed by this insect to support its heavier ovaries.

DISTRIBUTION. This subgenus is confined to the Mediterranean region.

INCLUDED SPECIES. Only one described species, *Gravenhorstia* (*Gravenhorstia*) *picta* Boie, is referable to this subgenus. Two females in the collections of the Hope Department of Entomology, Oxford, may represent a second species or it may be that these females are a rather smaller colour variant of *picta*.

Subgenus *KOKUJEWIELLA* Shestakov **stat. n.**

Kokujewiella Shestakov, 1926 : 257. Type-species: *Kokujewiella vicaria* Shestakov, 1926 : 258, by monotypy.

Nenethes Ceballos, 1957 : 8. Type-species: *Nenethes iberus* Ceballos, 1957 : 9, by monotypy. **Syn. n.**

Surface of the eye with short pubescence; lower face flat. Clypeus apically rounded, marginate, with at the most an indistinct median tooth; mandible from subequally bidentate to, with lower tooth distinctly the shorter, sometimes rather narrow, with at most a small basal flange. Genal carina reaching base of mandible and separate from hypostomal carina.

Mesoscutum evenly rounded, without any discernible trace of notauli; scutellum convex. Epicnemial carina indistinct, not reaching above 0·4 of mesopleuron, and with upper end distant from anterior margin of mesopleuron. Propodeum moderately short, posteriorly extended 0·5 of length of hind coxae.

Foreleg with basitarsus of ♂ (at least in *G. iberus*) almost equal in length with the fifth tarsal segment; first subdiscal cell explanate; 11–13 hamuli on vein R_1; 2 + 3*rm* proximal to 2*m–cu*.

CI = 1·05–1·35; BI = 1·65–2·00; DBI = 0·55–0·67; MI = 1·70–1·90; RI = 1·50–1·75; NI = 0·60–0·70; ICI = 2·40–4·50.

♂ genitalia. Aedeagus in profile medianly angled with large apicodorsal lobe, dorsally concave weakly; apicodorsal lobe dorsally membranous, membrane extending proximally to angulation; ventral membranous area weakly spinose, the anterior region produced into a small prominence which curves forward and up; ventral region not laterally extended (Text-fig. 110).

In most characters this subgenus is intermediate between *G.* (*Gravenhorstia*) and *G.* (*Erigorgus*).

DISTRIBUTION. Species of this subgenus are distributed throughout the Mediterranean region and Central Asia, approximately between 35°N and 45°N.

Included species. Two described species have been found to belong to this subgenus: *G.* (*Kokujewiella*) *vicaria* (Shestakov) and *G.* (*Kokujewiella*) *ibera* (Ceballos).

Subgenus *ERIGORGUS* Foerster **stat. n.**

Erigorgus Foerster, 1868 : 146. Type-species: *Anomalon fibulator* Gravenhorst, 1829 : 681, by subsequent designation (Perkins, 1962 : 422).

Sympratris Foerster, 1868 : 146. Type-species: *Anomalon ferrugineus* Norton, 1863 : 363 (included by Viereck, 1917 : 285), by subsequent monotypy.

Paranomalon Viereck, 1912*b* : 175. Type-species: *Ophion flavifrons* Gravenhorst, 1829 : 1088, by original designation.

Surface of eye glabrous; lower face flat. Clypeus rounded or centrally pointed, with or rarely without a median apical tooth; mandible with upper tooth distinctly the longer, basally with at most a minute swelling. Genal carina reaching mandible at same point as hypostomal carina.

Mesoscutum evenly rounded without any trace of notauli; scutellum weakly convex or deplanate. Epicnemial carina very short, usually not extending above lower corner of pronotum, upper end distant from anterior margin of mesopleuron. Propodeum quite short, posteriorly extended 0·45–0·55 of length of hind coxae.

Foreleg with basitarsus of ♂ at least 2·0 times as long as fifth tarsal segment; first subdiscal cell explanate; 10–14 hamuli on R_1; 2 + 3*rm* proximal or opposite *2m–cu*.

CI = 1·00–2·00; BI = 1·40–2·15; DBI = 0·50–0·66; MI = 1·30–2·00; RI = 1·30–1·98; NI = 0·80–1·55; ICI = 2·50+.

♂ genitalia. Aedeagus in profile medianly angled apically with a large dorsal lobe, dorsally concave; apicodorsal lobe membranous, ventral spinose membranous area present; aedeagus laterally almost evenly sclerotized; ventral region not laterally extended (Text-figs 108, 109).

This subgenus has been interpreted quite differently by various authors. Schmiedeknecht (1936) included a number of species, all of which have been found to be congeneric with the type-species, but excluded species of the *Anomalon cerinops*-group (*Paranomalon*). These he placed in the genus *Anomalon* (sensu Jurine). The distinction between these two groups was considered to be the position of vein 2 + 3*rm* in relation to *2m–cu*. Amongst the former group these veins were described as 'being continuous', whilst in the latter group *2m–cu* was said to be 'beyond' the cubital cross vein (2 + 3*rm*). No further differences have been found between the two groups, and as the position of vein 2 + 3*rm* is a particularly variable character, it is suggested that the *A. cerinops* group should not be accorded higher taxonomic distinction and be included within the subgenus *Erigorgus*.

Distribution. This subgenus is recorded from all regions except the Ethiopian.

Included species. This subgenus contains the majority of the described species of *Gravenhorstia*. The following have been examined:

Gravenhorstia (*Erigorgus*) *barbarica* (Morley), *G.* (*Erigorgus*) *cerinops* (Gravenhorst), *G.* (*Erigorgus*) *coreensis* (Uchida), *G.* (*Erigorgus*) *fibulator* (Gravenhorst), *G.* (*Erigorgus*) *melanops* (Foerster), *G.* (*Erigorgus*) *melanobata* (Gravenhorst), *G.* (*Erigorgus*) *ruficornis* (Szépligeti), *G.* (*Erigorgus*) *similis* (Szépligeti), *G.* (*Erigorgus*) *villosa* (Gravenhorst), *G.* (*Erigorgus*) *erythrocera* (Cameron), *G.* (*Erigorgus*) *interstitialis* (Cameron), *G.* (*Erigorgus*) *pilosella* (Cameron), *G.* (*Erigorgus*) *variornata*

(Cameron), *G.* (*Erigorgus*) *buccata* (Morley), *G.* (*Erigorgus*) *sonorensis* (Cameron) and *G.* (*Erigorgus*) *nigrita* (Norton) **comb. n.**

Subgenus ***RIBASIA*** Ceballos **stat. n.**

Ribasia Ceballos, 1921 : 49. Type-species: *Ribasia erythrogaster* Ceballos, 1921 : 49, by original designation.

Eye surface glabrous; lower face flat, coarsely punctate. Clypeus medianly pointed, without a median apical tooth; mandible slender, lower tooth much shorter than upper, with a conspicuous basal flange. Genal carina reaching base of mandible separate from hypostomal carina.

Mesoscutum evenly rounded, without any trace of notauli; scutellum strongly convex. Epicnemial carina indistinct, reaching a little above the lower corner of the pronotum, its upper end widely separated from the anterior margin of the mesopleuron. Propodeum quite short, posteriorly extended to reach 0·4 of length of hind coxae.

Foreleg with basitarsus of ♂ more than 3·0 times as long as fifth tarsal segment; first subdiscal cell explanate; 12 hamuli on vein R_1; 2 + 3*rm* distal to *2m–cu*.

CI = 1·25; BI = 1·65; DBI = 0·57; MI = 1·85; RI = 1·42; NI = 0·55; ICI = 3·00.

♂ genitalia. It has not been possible to examine the genitalia of this subgenus as only two specimens are known.

Apart from the form of the clypeus and mandibles this species is closely related to *G.* (*Gravenhorstia*) and *G.* (*Kokujewiella*). In *G.* (*Kokujewiella*) *vicaria* the mandibles are very similar to *G.* (*Ribasia*) *erythrogaster* except that the basal lobe in the former species is considerably smaller.

Distribution. This subgenus is recorded only from Spain.

Included species. Only the type-species *G.* (*Ribasia*) *erythrogaster* is known to belong to this genus.

The three subgenera *Gravenhorstia*, *Kokujewiella* and *Ribasia* collectively contain only four species, three of which are known from relatively few specimens. These subgenera appear to be mainly Mediterranean, but as this area is comparatively well worked entomologically and these species are taken so very rarely it is possible that this region represents the periphery of their range. Evidence for this in one species may be deduced from the following data.

G. (*Kokujewiella*) *ibera* (Ceballos): 1 ♂ Spain, 1 ♂ Israel, 3 ♀, 2 ♂ Turkey and 6 ♀, 5 ♂ southern U.S.S.R. (these figures represent the total known specimens to date). It is apparent that this species is more common in eastern districts and it is possible that the centre of distribution of these subgenera could be Central Asia. Until the fauna of this region is more fully known it is convenient to treat these groups as separate subgenera, but it is possible that the subgenera *Kokujewiella* and *Ribasia* may one day be included within the subgenus *Gravenhorstia*.

Genus ***AUBERTIANA*** Viktorov

Aubertia Viktorov, 1968 : 910. Type-species: *Romanella unidentator* Aubert, 1964 : 35, by original designation. [Homonym of *Aubertia* Oberthür, 1896.]

Aubertiana Viktorov, 1970 : 308. [Replacement name for Aubertia Viktorov.]

Eye without pubescence, margins ventrally parallel; occipital carina complete, close to posterior ocelli; frons without a median vertical carina. Antennae short, scape truncate, rather globose, 2·0 times as long as pedicel. Clypeus apically concave, without a median tooth; mandibles unidentate; labial palpi with four segments. Genal carina reaching base of mandible separate from hypostomal carina.

Pronotum dorsally long, subhorizontal, with transverse furrow; posterior corner flat, not covering spiracular sclerite; lower anterior margin of pronotum without a tooth, lower corner acute. Anterior of mesoscutum almost evenly rounded, but with a longitudinal concavity just before anterior margin; notauli absent; medio-posterior region of mesoscutum punctate; transverse suture of mesoscutum absent, transverse furrows absent. Epicnemial carina short, not extending above the lower corner of the pronotum, its upper end distant from anterior margin of mesopleuron, medio-ventrally not produced into a flange; sternaulus indistinct; posterior transverse carina of mesosternum broadly absent before each mid coxa.

Fore coxae smooth; fore tibial spur with numerous acute macrotrichia along inner face. Mid tibia with two apical spurs. Hind trochanter about 1·5 times as long as trochantellus; hind tarsi of ♂ not explanate; hind tarsal claws curved, pectinate to apices.

Forewing with *Rs* weakly bowed; 2 + 3*rm* opposite 2*m–cu*; 1*m–cu* and Cu_{1a} basally separated. Hindwing with 13 hamuli on R_1; distal abscissa of Cu_1 present.

CI = 1·15*; BI = 1·90*; DBI = 0·60*; MI = 2·00*; RI = 1·60*; NI = 1·10*; ICI = 6·00*.

Propodeum reticulate, spiracles more than 4·5 times as long as broad; apex of propodeum reaching 0·3 of length of hind coxae; gaster compact (DAI = 1·30; LAI = 2·30).

♀ unknown.

♂ genitalia. Insufficient material available for dissection.

This genus appears to be closely related to the subgenus *Gravenhorstia* from which it differs principally in the form of the clypeus and mandibles. Clypeo-mandibular variation is particularly common within the genus *Gravenhorstia* and it is possible that this species may better be placed within it. However, two features of this species are not found in *Gravenhorstia*. The hind tarsal claws of the holotype (♂) are pectinate to the apices, unlike males of *Gravenhorstia* which have the hind tarsal claws long and simple. The anterior of the mesoscutum has a very characteristic longitudinal depression or concavity immediately behind the anterior margin. A similar concavity has not been observed in *Gravenhorstia* species, therefore *Aubertiana* is retained as a separate genus next to *Gravenhorstia*.

Distribution. This genus is found in the North African region.

Included species. Only the type-species, *A. unidentator* (Aubert), is at present referable to this genus.

Genus ***ATROMETOIDES*** Fahringer

Atrometoides Fahringer, 1922 : 7. Type-species: *Atrometoides winkleri* Fahringer, 1922 : 8, by monotypy.

Romanella Meyer, 1935 : 114. Type-species: *Romanella maracandica* Meyer, 1935 : 115, by monotypy.

Nothing further can at present be added to the descriptions of this genus included by Townes (1971).

It would appear that this genus is closely related to *Aubertia*, and to the subgenus *G.* (*Kokujewiella*).

Genus *PORIZONOPTERON* Meyer

Porizonopteron Meyer, 1931 : 7. Type-species: *Porizonopteron schestakovi* Meyer, 1931 : 7, by monotypy.

Eye with surface glabrous; inner margins subparallel; occipital carina complete, close to posterior ocelli; frons with a median vertical carina. Antenna very short, ♀ without a white band; scape truncate, about 1·3 times as long as pedicel; fourth flagellar segment 1·2 times as long as broad. Clypeus with a weak median apical tooth; mandibles with lower tooth vestigial or absent. Genal carina joining base of mandible at same point as hypostomal carina.

Pronotum dorsally of moderate length, subhorizontal, without a transverse furrow, posterior corner not covering spiracular sclerite; lower anterior margin without a tooth, lower corner truncate. Anterior of mesoscutum abruptly rounded, apically flattened; notauli absent; medio-posterior region of mesoscutum punctate; transverse suture of mesoscutum absent, transverse furrows absent. Epicnemial carina with upper end reaching posterior margin of pronotum just below middle of mesopleuron, medioventrally not raised; sternaulus absent; posterior transverse carina of mesosternum interrupted before each mid coxa.

Fore coxae smooth; fore tibial spur rather long, with sparsely distributed macrotrichia on inner surface. Mid tibia bicalcarate. Hind trochanter subequal in length to a ventrally flattened trochantellus; hind tibia laterally compressed, hind basitarsus with a laterally compressed postero-dorsal prolongation (Text-fig. 251); hind tarsal claws of ♂ weakly curved, simple.

Forewing with *Rs* more or less straight; 2 + 3*rm* proximal to 2*m–cu*; 1*m–cu* and Cu_{1a} basally separate. Hind wing with seven hamuli on vein *R*1; distal abscissa of Cu_1 present, faint, not reaching margin of wing.

CI = 0·75*; BI = 1·30*; DBI = 0·70*; MI = 1·40*; RI = 2·20*; ICI = 0·40*; NI = 1·80*.

Propodeum weakly coriaceous, spiracle about 4 times as long as broad; apex of propodeum extended 0·8 of length of hind coxa. Gaster elongate.

♂ genitalia. Aedeagus in profile apically swollen, truncate, with dorsal membranous area extended anteriorly, and with extensive ventral membranous area bearing weak spines (Text-fig. 252).

The holotype and only known specimen of *P. schestakovi* has been destroyed. A second species *P. metatarsator* Shaumar, 1966 (= *Anomalon paradoxum* Schmiedeknecht, 1900, junior primary homonym of *A. paradoxum* Brauns, 1895) is represented in the collections of the BMNH by a single ♂, from which the above description is made.

P. schestakovi, as figured by Meyer (1931: fig. 2), has the basitarsus intermediate in form between *P. metatarsator* and species of *Barylypa*. Apart from the form of the hind legs and differences in the aedeagus both species are similar to some species of *Barylypa*.

Distribution. Species of this genus are recorded from arid regions, *P. schestakovi* from southern U.S.S.R., *P. metatarsator* from Egypt, Algeria (Oran) and Saudi Arabia.

Included species. *P. schestakovi* Meyer and *P. metatarsator* Shaumar.

Genus *TRICHOMMA* Wesmael

Trichomma Wesmael, 1849 : 119. Type-species: *Anomalon* (*Trichomma*) *fulvidens* Wesmael, 1849 : 139, by monotypy.

Trichomella Szépligeti, 1910 : 91. Type-species: *Trichomma clavipes* Krieger, 1904 : 166, by subsequent designation (Viereck, 1914*a* : 148).

Eye with surface elongately and densely hirsute, the hairs longer than their distance apart basally; inner margins very strongly convergent ventrally; occipital carina complete, close to posterior ocelli; frons without a median vertical carina or lamella (except in one western Palaearctic species). Antennae moderately long, ♀ without white bands; scape truncate, about 1·1 times as long as pedicel; fourth flagellar segment about 3·0 times as long as broad. Clypeus with apex medianly pointed, rarely truncate, always with at least a small apical tooth centrally; mandibles bidentate, not twisted, lower tooth slightly shorter than upper tooth; labial palpi with three, rarely four segments, cardo basally lobate. Genal carina joining base of mandible sometimes meeting hypostomal carina at same point.

Pronotum dorsally long, subvertical, without a transverse furrow, posterior corner not covering spiracular sclerite; lower anterior margin without a tooth but with a blunt tubercle at base of epomia, lower corner truncate. Anterior of mesoscutum abruptly rounded without an apical concavity; notauli variable, usually quite strongly impressed past the centre of mesoscutum, but in some species indistinct or absent; medio-posterior region of mesoscutum usually somewhat rugose; transverse suture of mesoscutum absent, transverse furrows absent. Epicnemial carina reaching to or just below centre of mesopleuron, its upper end reaching anterior margin of mesopleuron, medio-ventrally not or weakly raised; sternaulus absent; posterior transverse carina of mesosternum usually interrupted in front of each mid coxa, rarely complete.

Fore coxae smooth, but rather angular; fore tibial spur with a very few acuminate macrotrichia on inner surface. Mid tibia with two spurs. Hind trochanter more than 2·0 (often more than 3·0) times as long as trochantellus; hind tarsi of ♂ not swollen; hind tarsal claws curved, pectinate to or beyond centre, not obviously sexually dimorphic.

Forewing with *Rs* weakly sinuate to almost straight; 2 + 3*rm* proximal to 2*m–cu*; 1*m–cu* and Cu_{1a} basally separate. Hind wing with 6–10 hamuli on vein R_1; distal abscissa of Cu_1 absent, or in large species with vein represented by a stub and an area of pigmentation in wing membrane, or rarely as a distinct vein, but not joining *cua*, extremely rarely present and continuous.

CI = 0·40–1·03; BI = 1·20–1·55; DBI = 0·60–0·79; MI = 1·42–2·12; RI = 0·85–1·40; ICI = 0·90–5·00; PI = 1·64–2·75.

Propodeum reticulate, spiracle subcircular to 2·0 times as long as broad; apex of propodeum not extended beyond 0·5 of length of hind coxae. Gaster elongate.

♀ genitalia. Valvula 3 from 1·0–2·3 times as long as tergite 3; apex of ovipositor abruptly constricted, constricted part about 5·0 times as long as median thickness of ovipositor; extreme apex decurved; ovipositor not at all laterally compressed; nodus distinct, raised and heavily sclerotized (Text-fig. 20).

♂ genitalia. Single syntergum present; ninth abdominal sternite quadrate, posterior margin with a median impression; gonosquamae short, truncate; gonolaciniae distally abruptly angled about 95°; teeth reduced to ridges; apodeme straight, extending about 0·5 of length of basivolsellar strut or 0·8 of length of basivolsellar strut in Australian species. Distivolsella slender, basally 0·3 times as wide as long; clasping face centrally swollen, swelling bearing elongate spines. Paramere proximally swollen apically, impressed. Aedeagus in profile swollen, distal apex impressed, dorsally convex, very membranous; extreme distal apex bearing spines; ventral surface covered with minute spinules, not laterally extended (Text-figs 56, 65, 92, 130, 131).

One of the most characteristic features of this genus is the possession of long hairs on the surface of the eyes. Investigation of the surface of the compound eye has shown it to be composed of many small, almost rectangular facets, with broad undifferentiated interfacetal cuticular areas which bear the elongate pubescence. Most other genera in this subfamily have the more usual arrangement of hexagonal facets with small interfacetal cuticular areas. Only in a few species are the compound eyes obviously hairy and in these species the pubescence is

shorter and sparser than that of *Trichomma*. The reduction in the visual surface of the compound eye of *Trichomma* may be the result of a difference in the host preference between this species and other Therionini (the biology of many species is unfortunately unknown at present). *Trichomma* species are frequently found as parasites of fruit-mining lepidopterous larvae (Rosenberg, 1934) whereas all other well known Therionini are parasitic upon free living lepidopterous larvae. It is therefore conceivable that the adult *Trichomma* may rely less on vision to locate a prospective host than do other Therionids. Alternatively the hairs on the eyes may serve to protect the eye surface. Similar elongate hairs on the eye surface of Asilidae have been described by Oldroyd (1964) as providing protection against prey damage. There is, however, no observed occurrence in the life history of the adult *Trichomma* to account for why the eye surface should need more protection than that of any other Therionini.

The form of the male genitalia of this genus at first appeared to be quite unlike that of any other genus. Further study of many species from widely separated regions revealed that there are undoubted affinities between this genus and *Heteropelma* and *Tanypelma*. In the majority of *Trichomma* species the distivolsellae have long spines arranged centrally on a raised hump, but in the Australian species, *T. elegantulum*, there are long spines arranged on a somewhat 'lopsided' hump (Text-fig. 92) and a few shorter spines proximally positioned. This type of distivolsella is intermediate in structure between that of *Heteropelma* and typical *Trichomma*. There is also a marked resemblance between the gonolaciniae of *Trichomma* and *Tanypelma*. The gonolacinia of *Trichomma elegantulum* cannot be distinguished from that of *Tanypelma datanae* as both have abruptly angled apices with teeth reduced to ridges and elongate apodemes (Text-fig. 55). There is also a resemblance between the aedeagal apices of species belonging to these three genera.

Short (1959 : 506) mentions that Dr Perkins had directed his attention to two reared specimens of *T. occisor*, in the collections of the BMNH, with quite a well developed cocoon. Anomaloninae are generally considered not to make a cocoon and these examples of a species of *Trichomma* spinning a cocoon are unique. The cocoons have been opened at some date and the contents removed although there is no indication on the specimens as to who did this examination or where the contents could be. Examination of the BMNH slide collections has revealed that there is a single slide bearing the label '*Trichomma occisor* B.M. coll' and underneath '? Campoplegid' in different ink and written with a different pen, though probably by the same person. The larval cephalic capsule on the slide is not an Anomalonid as the hypostomal spurs are present and very long, the epistomal arch is centrally absent, and there is a Y-shaped prelabral sclerite discernible. The cephalic capsule on this slide is thought to be that of the final instar larva of *Charops* species. Normally *Charops* species make a distinctive black and white cocoon, but occasionally specimens have been found to emerge from unicolorous brown cocoons, similar to those appended to the specimens of *T. occisor*. If the specimen on the slide was extracted from the cocoon appended to *T. occisor* then undoubtedly these are not cocoons from which the specimens of *T. occisor* emerged. Further evidence is needed before it can be accepted that any Anomaloninae larvae construct cocoons.

The immature stages of *Trichomma* are far more similar to those of the 'Theriine' genera than they are to most other genera. The eggs of *Trichomma* are lamp-shaped, like those of *Therion*, *Heteropelma*, *Tanypelma* and *Habronyx* (Text-figs 96–98). The final instar larvae of *Trichomma* have the cephalic capsule with a short hypostoma, approximately as long as the breadth of the mandibular base, similar to that of *Therion* (Text-figs 143, 145). The cephalic capsule of *Trichomma* differs from those of other known genera in having the stipital sclerite weakly bifurcate.

Although *Trichomma* adults are morphologically very unlike the 'Theriine' genera it is difficult to explain the similarities between these genera observed in the immature stages and genitalia structure other than by assuming that there is a definite phylogenic affinity.

Distribution. This is a cosmopolitan genus but species constitute a more noticeable part of the Anomalonine fauna in the Indo-Papuan and Australian regions where species have been reared from the pupae of a variety of economically important Lepidoptera.

Included species. The following species were examined:

T. fulvidens Wesmael, *T. occisor* Habermehl, *T. enecator* (Rossi), *T. intermedium* Krieger, *T. biroi* (Szépligeti), *T. clavipes* Krieger, *T. decorum* (Cameron), *T. elegantulum* Turner, *T. insularis* Szépligeti, *T. nigricans* Cameron, *T. albicoxum* Morley and at least six further undescribed species.

Genus ***AGRYPON*** Foerster

Agrypon Foerster, 1860 : 151. Type-species: *Ophion flaveolatus* Gravenhorst, 1807 : 268, by subsequent designation (Morley, 1913 : 424).

[*Labrorychus* Foerster, 1868 : 146, sensu auct. Misidentification.]

Trichonotus Cameron, 1905*a* : 124. Type-species: *Trichonotus reticulatus* Cameron, 1905*a* : 124, by monotypy. [Homonym of *Trichonotus* Schneider, 1801.] **Syn. n.**

Trichionotus Cameron, 1905*b* : 168. Type-species: *Trichionotus reticulatus* Cameron, 1905*b* : 168 [= *Trichonotus reticulatus* Cameron, 1905*a* : 124], by monotypy. **Syn. n.**

Odontagrypon Cameron, 1906 : 90. Type-species: *Odontagrypon spilonotus* Cameron, 1906 : 91, by monotypy.

Paragrypon Uchida, 1941 : 159. Type-species: *Gongropelma kikuchii* Uchida, 1928 : 258, by original designation. **Syn. n.**

Dioborus Rao, 1953 : 204. Type-species: *Dioborus indica* Rao, 1953 : 204 [= *Agrypon nox* Morley, 1913*a* : 91], by original designation. **Syn. n.**

Eye with surface glabrous, margins weakly to strongly convergent ventrally; occipital carina usually present, close to posterior ocelli; frons with or without a median vertical carina. Antennae short to very long, those of ♀ without a white band; scape truncate, at least 1·3 times longer than pedicel; fourth flagellar segment about 3·0 times as long as broad. Clypeus with apex pointed centrally, with a single median tooth; mandibles apically bidentate, lower tooth distinctly the shorter, apices not twisted (except in a few Palaeotropical species which have the apices strongly twisted 70°); labial palpi with three or four segments; cardo basally lobate. Genal carina joining base of mandible.

Pronotum dorsally long, subvertical, with or without a weak transverse furrow, posterior corner at most occluding 0·5 of spiracular sclerite; lower anterior margin without a tooth,

lower corner truncate. Anterior of mesoscutum abruptly rounded without an apical concavity; notauli variable, usually strongly impressed, rarely absent entirely; medio-posterior region of mesoscutum punctate, coriaceous or rugose; transverse suture of mesoscutum usually absent, in a few species present except laterally, very rarely complete; transverse furrows present or absent. Epicnemial carina various, usually present, reaching above lower corner of pronotum and parallel to the anterior margin of the mesopleuron; epicnemial carina medio-ventrally weakly produced, in some species strongly raised into a lamella; posterior transverse carina of mesosternum either interrupted in front of each mid coxa or complete.

Fore coxae either smooth or with a carina on anterior or anterio-medial surfaces, rarely with the carina present as discontinuous flecks or very weakly impressed; fore tibial spur with numerous subacute macrotrichia on inner surface. Mid tibia with two spurs. Hind trochanter about 1·2 times as long as trochantellus; hind tarsi of ♂ not or weakly swollen; hind tarsal claws curved, pectinate to about centre, not obviously sexually dimorphic.

Forewing with vein *Rs* almost straight; *2 + 3rm* proximal to *2m–cu*; *1m–cu* and Cu_{1a} basally separated from each other but usually very close together. Hindwing with 9–12 hamuli on vein R_1; distal abscissa of Cu_1 present or absent.

CI = 0·15–0·60; BI = 1·20+; DBI = 0·50–0·65; MI = 1·40–1·80; RI = 0·95–1·35; ICI = 1·30–3·70.

Propodeum reticulate, spiracles very variable in shape; apex of propodeum reaching about 0·5 of length of hind coxae. Gaster elongate.

♀ genitalia. Valvula 3 from a little longer than apical abdominal depth to 1·2 times as long as tergite 3; ovipositor abruptly constricted, elongately pointed; extreme apex decurved; ovipositor a little compressed laterally (Text-fig. 26).

♂ genitalia. Single syntergum usually present, rarely with separate syntergites; ninth abdominal sternite transverse, posteriorly truncate; gonosquamae short, truncate. Gonolaciniae distally abruptly angled about 70°; teeth small; apodeme approximately straight, reaching about 0·5 of length of basivolsellar strut. Distivolsella moderately slender, basally 0·55 times as wide as long; clasping face concave with a diagonal ridge bearing teeth. Paramere proximally acutely pointed. Aedeagus in profile variable, usually apically expanded with distal apex truncate, with or without a small protruberance, dorsally flat or slightly convex, or rarely weakly concave, very membranous; ventral region laterally produced, weakly to very strongly; lateral sclerotized area not or just reaching apex, always angled downwards near tip (Text-figs 90, 129).

Previously this genus has been interpreted in different ways. Some authors (Schmiedeknecht, 1936; Morley, 1915; etc.) did not consider the fore coxal carina an important feature but divided the species now placed in this genus between *Labrorychus* sensu auct. and *Agrypon* solely on whether or not the distal abscissa of Cu_1 was present (a character which has been found to be very variable, even within a single population). Townes (1971) included *Labrorychus* sensu auct. and most of *Agrypon* sensu classical authors within *Trichionotus*. The only constant feature permitting separation of *Trichionotus* from *Agrypon* s. str. is the form of the fore coxae. A short series of specimens of an undescribed species from New Guinea in the collections of the BMNH show variation in the form of the fore coxa, with the carina more discernible in the female and entirely absent in some males. In some specimens from SE. Asia the fore coxal carinae are discontinuous, very weak or present only apically. It is apparent that all species are better included within a single genus as suggested above.

This is a very large genus, with a considerable range of variation between the species. A number of species may be outstanding in having one obviously unusual feature (such as smooth fore coxae or apically twisted mandibles) but it is not

concomitant with the classification of the group as a whole to accord these species higher taxonomic status at present.

Distribution. This genus is cosmopolitan, but is particularly numerous both in species and in numbers of individuals in the Palaearctic region. Species are less common in the Australian and Papuan regions where they tend to be replaced in part by *Trichomma* species and *Perisphincter* species respectively.

Included species. The following species have been found to be referable to this genus:

A. flaveolatum (Gravenhorst), *A. anxium* (Wesmael), *A. brevicolle* (Wesmael), *A. clandestinum* (Gravenhorst), *A. debilis* (Wesmael), *A. elongatus* Uchida, *A. flavifrons* (Smith), *A. flexorius* (Thunberg), *A. hilare* (Tosquinet), *A. polyxenae* (Szépligeti), *A. stenostigma* Thomson, *A. suzukii* (Matsumura), *A. tenuicorne* (Gravenhorst), *A. varitarsum* (Wesmael), *A. anomelas* (Gravenhorst), *A. coarctatum* (Brullé), *A. dozense* Cheesman, *A. falcator* (Smith), *A. ferrugineum* Morley, *A. fuscicorne* (Cameron), *A. indicum* Szépligeti, *A. nigricans* Szépligeti, *A. nox* Morley, *A. omabense* Cheesman, *A. productor* (Morley), *A. reticulatum* (Cameron), *A. agnatum* (Cresson), *A. albiditarsum* Morley, *A. flaviceps* Cameron, *A. lineiger* Morley, *A. postscutellare* Morley, *A. residuum* Cresson, *A. ruficaudatum* Morley, *A. africanum* (Morley), *A. primum* Morley, *A. secundum* Morley, *A. spilonotum* (Cameron), *A. delarvatum* (Gravenhorst) **comb. n.**, *A. minutum* Bridgman **stat. rev.** and a large number undescribed.

Genus ***PERISPHINCTER*** Townes

Perisphincter Townes, 1961 : 474. Type-species: *Agrypon tisiphone* Morley, 1913*a* : 92, by original designation.

Eye without pubesence, moderately convergent ventrally; occipital carina complete, close to posterior ocelli; frons without a median vertical carina. Antennae moderately long to long, those of ♀ without a white band; scape truncate, 2·0 times as long as pedicel; fourth flagellar segment about 3·5 times as long as broad. Apex of clypeus with or without a median apical tooth, sometimes with a pair of weak lateral teeth, sometimes simply convex; mandibles bidentate, lower tooth distinctly the shorter, apices not twisted; labial palpi with three segments; cardo basally lobate. Genal carina reaching base of mandible.

Pronotum dorsally of moderate length, subvertical, with a transverse furrow that is centrally obsolescent; posterior corner not occluding spiracular sclerite; lower anterior margin without a tooth, lower corner truncate. Mesoscutum anteriorly abruptly rounded, without a concavity; notauli represented by rugose area; medio-posterior region of mesoscutum rugose; transverse suture of mesoscutum absent, transverse furrows absent. Epicnemial carina reaching to centre of mesopleuron, upper end reaching anterior margin of mesopleuron; epicnemial carina medio-ventrally weakly raised into flange; sternaulus indistinct; posterior transverse carina of mesosternum complete.

Fore coxae encircled by a carina, on the outer side with the carina present above the trochanteral socket; fore tibial spur with numerous acute macrotrichia along inner face. Mid tibia with two spurs. Hind trochanter about 1·2 times as long as trochantellus; hind tarsi of ♂ not swollen; hind tarsal claws short, curved and pectinate almost to apices, not obviously sexually dimorphic.

Forewing with vein *Rs* almost straight; 2 + 3*rm* proximal to 2*m–cu*; 1*m–cu* and Cu_{1a} basally separated from each other, but usually very close together. Hindwing with 7–9 hamuli on vein R_1; distal abscissa of Cu_1 absent.

CI = 0·10–0·25*; BI = 1·25–1·40*; DBI = 0·60–0·75*; MI = 2·20–2·45*; RI = 1·50–1·80*; PI = 2·30–2·70*; ICI =, 1·10–1·25*.

Propodeum reticulate, spiracle from subcircular to 1·5 times as long as broad; apex of propodeum reaching about 0·5 of length of hind coxae; gaster elongate.

♀ genitalia. Valvula 3 from a little longer than apical abdominal depth to 0·7 of length of tergite 3; apex of ovipositor constricted, constricted part about 3·0 times as long as thickness of ovipositor medially; extreme apex decurved; ovipositor weakly laterally compressed, sometimes entire ovipositor decurved.

♂ genitalia. Separate syntergites present; ninth abdominal sternite transverse posteriorly truncate; gonosquamae short, truncate; gonolaciniae distally evenly rounded about 80°; teeth indistinct; apodeme straight, reaching 0·3 of length of basivolsellar strut. Distivolsella slender, basally 0·5 times as wide as long; clasping face flat, teeth scattered diagonally. Paramere proximally rounded. Aedeagus in profile weakly angled, apically rounded, dorsally with apical swelling, otherwise rather flat; membranous except for sclerotized lateral region which is decurved apically, reaching the aedeagal margin at apicoventral corner; ventral membranous region extended laterally (Text-figs 76, 127).

This genus is little more than a rather uniform group of *Agrypon* species, but as it is quite possible at present to separate reliably these two groups they have been retained as distinct genera.

Distribution. *Perisphincter* species occur mainly in the Indo-Papuan region where to a large extent they replace *Agrypon* species. Townes tentatively refers a single Neotropical species to this genus. An undescribed species is known to occur in Australia.

Included species. Of the three described species only *P. tisiphone* (Morley) is known to the author. Seven undescribed species have also been examined.

Genus *PHAENOLABRORYCHUS* Viereck

Phaenolabrorychus Viereck, 1914*b* : 379. Type-species: *Phaenolabrorychus anisitsi* Viereck, 1914*b* : 379, by original designation.

Eyes with very sparse short pubescence, which is often difficult to observe; occipital carina complete, close to posterior ocelli; frons with an indistinct median vertical carina. Antennae long, those of ♀ without a white band, scape truncate, 0·8–0·9 times as long as pedicel, fourth flagellar segment about 3·0 times as long as broad; apex of clypeus with two acute teeth; mandible bidentate, lower tooth distinctly the shorter, apices twisted about 15°; labial palpi with three segments; cardo basally lobate. Genal carina joining base of mandible close to hypostomal carina.

Pronotum moderately long dorsally, subvertical, with transverse groove which is centrally wanting, posterior corner occluding about 0·3 of spiracular sclerite; lower anterior margin of pronotum without a tooth, but with a tubercle at base of epomia, lower corner truncate. Anterior of mesoscutum abruptly angularly rounded, with trace of an apical concavity; notaulus distinct, reaching to hind margin of mesoscutum; medio-posterior area of mesoscutum coriaceous; transverse suture of mesoscutum absent, transverse furrows distinct and obvious. Epicnemial carina reaching above centre of mesopleuron, angled apically to reach anterior margin of mesopleuron; sternaulus impressed as a broad groove; epicnemial carina medioventrally raised into a small lamella; posterior transverse carina of mesosternum complete.

Fore coxae almost flat beneath, the flattened area bounded by an anterior/anterio-medial carina; fore tibial spur with numerous acute macrotrichia along inner face. Mid tibia with

two apical spurs. Hind trochanter 1·8 times as long as trochantellus; hind tarsi of ♂ not swollen; hind tarsal claws short, curved, pectinate to apices, not obviously sexually dimorphic.

Forewing with *Rs* straight; 2 + 3*rm* proximal to 2*m–cu*; 1*m–cu* and Cu_{1a} basally separate, but close together, hindwing with 7–9 hamuli on R_1; distal abscissa of Cu_1 absent.

CI = 0·15–0·25; BI = 1·90–2·10; DBI = 0·80–0·85; MI = 2·10–2·50; RI = 1·10–1·25; PI = 5·30–5·50; ICI = 1·10–1·20.

Propodeum reticulate, spiracle subcircular, unusual in being angled in surface of propodeum so that plane of spiracular aperture is horizontal; propodeum posteriorly produced into 'neck' which is unsculptured and reaches about 1·40 of length of hind coxae. Gaster elongate.

♀ genitalia. Valvula 3 0·6 times as long as tergite 3; apex of ovipositor slightly sinuous, evenly acutely pointed, extreme apex obviously decurved; ovipositor not laterally compressed.

♂ genitalia. Syntergites not fused; ninth abdominal sternite transverse, posteriorly truncate; gonosquamae truncate, short. Gonolacinae distally evenly rounded about 75°; teeth small; apodeme straight, reaching about 0·4 of length of basivolsellar strut. Distivolsella slender, basally 0·5 times as wide as long; clasping face flat, teeth arranged diagonally on a weak ridge. Paramere proximally acute. Aedeagus in profile weakly angled, apically truncate, dorsally almost flat, membranous, ventrally laterally produced; sclerotized area not reaching aedeagal apex (Text-fig. 128).

This genus has been confused with *Agrypon* in the past (Townes & Townes, 1966) although in recent work (1971) Townes retained it as a separate genus. *Phaenolabrorychus* has been found to be distinct from *Agrypon* in a number of ways. The elongate unsculptured propodeal neck is a particularly obvious feature of this genus which is not found in *Agrypon* but there are also other consistant differences. The scape of *Phaenolabrorychus* is slightly shorter than the pedicel, whereas in *Agrypon* the scape is clearly longer than the pedicel (Text-fig. 171). *Phaenolabrorychus* is characterized by the possession of three deep furrows immediately in front of the scuto-scutellar groove, whereas in *Agrypon* there are usually no furrows present, and if furrows are present they are small and weakly impressed, quite unlike those of *Phaenolabrorychus* (Text-figs 178, 180). The shape of the clypeus, positioning of the petiolar spiracles and the form of the ovipositor of *Phaenolabrorychus* may also be used to distinguish this genus from *Agrypon*.

Distribution. This genus is apparently restricted to the Neotropical region.

Included species. Only one species, *P. anisitsi* Viereck, is referable to this genus at present.

Genus ***PARANIA*** Morley

Parania Morley, 1913*a* : 96. Type-species: *Parania nototrachoides* Morley, 1913*a* : 97 [= *Atrometus tricolor* Szépligeti, 1906 : 126], by monotypy.

Eye glabrous, ventrally convergent; occipital carina complete, close or moderately close to posterior ocelli, separated at a maximum by about 1·3 of ocellar diameter; frons without a median vertical carina. Antennae short to moderately long, those of ♀ without a white band; scape truncate, about 1·5 times as long as pedicel; fourth flagellar segment about 3·0 times as long as broad. Apex of clypeus acute, with a median tooth; mandible bidentate, lower tooth distinctly the shorter, apices not twisted; labial palps of three segments; cardo basally lobate. Genal carina joining base of mandible.

Pronotum dorsally moderately long, subvertical, with transverse furrow, posterior corner occluding about 0·4 of spiracular sclerite; lower anterior margin of pronotum without a tooth, lower corner truncate. Anterior of mesoscutum abruptly rounded, without an impressed

area; notaulus indistinct or absent; medio-posterior region of mesoscutum punctate; transverse suture of mesoscutum absent, transverse furrows absent. Epicnemial carina reaching to centre of mesopleuron, its upper end reaching anterior margin of mesopleuron; epicnemial carina medio-ventrally not produced; sternaulus absent; posterior transverse carina of mesosternum complete.

Fore coxae smooth; fore tibial spur with numerous acute macrotrichia on inner face. Mid tibia with two spurs. Hind trochanter about 2·0 times as long as trochantellus; hind tarsi of ♂ not swollen; hind tarsal claws weakly curved, moderately long, those of ♀ more curved and pectinate than those of ♂.

Forewing with *Rs* straight; 2 + 3*rm* proximal to 2*m–cu*; 1*m–cu* and Cu_{1a} basally fused; hindwing with 5–8 hamuli on R_1; distal abscissa of Cu_1 absent.

BI = 1·20–1·35; DBI = 0·50–0·72; MI = 1·30–1·68; RI = 0·67–0·80; ICI = 0·90–1·25; PI = 1·75–2·05.

Propodeum punctate, or weakly reticulate, spiracle circular to 2·0 times as long as broad; propodeum posteriorly reaching 0·7 of length of hind coxae. Gaster elongate.

♀ genitalia. Valvula 3 about 0·9 times as long as tergite 3; apex of ovipositor almost hastate, elongately acutely pointed, extreme apex decurved; ovipositor laterally compressed (Text-figs 7, 12, 29).

♂ genitalia. Single syntergum present; ninth abdominal sternite transverse, posteriorly truncate; gonosquamae short, subacute. Gonolacinae distally evenly curved about 50°; teeth large and conspicuous; apodeme straight, reaching 0·65 of length of basivolsellar strut. Distivolsella broad basally, 1·0 times as wide as long; clasping face flat with few scattered teeth. Paramere proximally broadened before tapering abruptly to an acute apex (Text-fig. 45). Aedeagus in profile straight, acutely pointed, with a minute dorsal membranous area and a long narrow ventral membrane that is not extended laterally (Text-figs 54, 74, 132).

Parania has previously gone under the name *Atrometus* until Townes (1971) pointed out that *Atrometus*, as represented by the type-species *A. insignis*, was quite a distinct genus. The majority of so-called *Atrometus* species were placed in *Parania* which previously had been included as a synonym of *Atrometus* (Townes & Townes, 1966).

Parania is a very distinctive genus and not at all as closely related to *Agrypon* as previous authors supposed (Morley, 1915). *Parania* has consistently fewer hamuli on vein R_1 than any of the 'Agryponine' genera (that is *Agrypon*, *Perisphincter* and *Phaenolabrorychus*) and has a significantly smaller value of RI. The most striking difference between *Parania* and the 'Agryponine' genera have been observed in the form of the female and male genitalia. The ovipositor of *Parania* is quite characteristic and unlike that of most other Therionini except to some extent *Pseudanomalon*. The aedeagus of *Parania* species is unique, no other specimen examined was found to have a straight apically acute aedeagus. The aedeagi of *Spolas* and *Clatha* are closest in structure to that of *Parania* and it is possible that reduction of the membranous area of a *Clatha*-type aedeagus could have resulted in the aedeagus of *Parania*. However, there are considerable macromorphological differences between species of these genera. The relationships between this and other genera are more fully discussed below.

Distribution. *Parania* is recorded from all regions except the Australian.

Included species. The following species were examined:

P. albopilosella (Cameron), *P. tricolor* (Szépligeti), *P. geniculata* (Holmgren) and two undescribed species.

Genus *SPOLAS* Townes

Spolas Townes, 1961 : 473. Type-species: *Atrometus flavifrons* Ashmead, 1901*b* : 352, by original designation.

Eyes glabrous or with sparse short hairs, margins weakly to strongly convergent ventrally; occipital carina complete, close to posterior ocelli, separated by not more than 1·0 of ocellar diameter; frons without a median vertical carina. Antennae moderately long, those of ♀ without a white band; scape subtruncate, sometimes flattened medianly, about 1·2 times longer than pedicel; fourth flagellar segment more than 7·0 times as long as broad. Apex of clypeus rounded with a median tooth, to subtruncate without a tooth; mandible bidentate, apices not or very slightly twisted, lower mandibular tooth distinctly the shorter; labial palps with three segments. Genal carina sinuate ventrally, parallel to hypostomal carina, which turns sharply along lower margin of hypostoma to join genal carina at base of mandible.

Pronotum dorsally narrow, subhorizontal, with transverse furrow, posterior corner with weak to strong dorsal flanges, partially occluding spiracular sclerite; lower anterior margin of pronotum without a tooth, lower corner rounded. Anterior of mesoscutum abruptly rounded, with weak median apical concavity; notaulus absent; medio-posterior region of mesoscutum densely and finely punctate; transverse suture of mesoscutum absent, transverse furrows absent. Epicnemial carina reaching above centre of mesopleuron, its upper end reaching anterior margin of mesopleuron; epicnemial carina medio-ventrally not produced; sternaulus present as a concavity; posterior transverse carina of mesosternum present only laterally as vestiges.

Fore coxae smooth; fore tibial spur with numerous acute macrotrichia on inner face. Mid tibia with two spurs. Hind trochanter about 1·2 times longer than trochantellus; hind tarsi of ♂ not swollen; hind tarsal claws curved, pectinate almost to apex, not obviously sexually dimorphic.

Forewing with *Rs* almost straight; 2 + 3*rm* proximal to 2*m–cu*; 1*m–cu* and Cu_{1a} basally separate, but close together. Hindwing with 4–6 hamuli on R_1; distal abscissa of Cu_1 absent.

CI = 0·20–0·35; BI = 1·20–1·45; DBI = 0·55–0·65; MI = 2·40–3·05; RI = 0·25–0·35; ICI = 1·10–1·33; PI = 1·75–2·50.

Propodeum coriaceous, spiracles circular or subcircular; propodeum posteriorly reaching 0·3 of length of hind coxae. Gaster elongate.

♀ genitalia. Valvula 3 a little longer than apical depth of abdomen; apex of ovipositor elongately pointed, extreme apex weakly decurved; ovipositor weakly laterally compressed; unusual in having a dorsal subapical swelling that is large and convex.

♂ genitalia. Single syntergum present; ninth abdominal sternite transverse and truncate posteriorly; gonosquamae short, acute. Gonolaciniae evenly rounded distally about 80°; teeth small; apodeme straight, reaching 0·5 of length of basivolsellar strut. Distivolsella moderately broad, basally 0·6 times as wide as long, clasping face flat, teeth arranged peripherally. Parameres proximally spatulate (Text-fig. 46). Aedeagus in profile weakly decurved, apically acute, dorsal membranous area present, ventral membranous area absent, lateral sclerotized area extending apically; ventral margin of aedeagus laterally extended into triangular regions (Text-figs 58, 81, 82, 133).

This distinctive genus is at once recognizable by the elongate basal flagellar segments, the dorsal pronotal flanges (Text-fig. 203), and the very small value of RI.

Distribution. Hitherto this genus was recorded only from the Hawaiian Islands but in the collections of the BMNH are two males, one from Ohakun, New Zealand (coll. T. R. Harris) and one from Nelson, New Zealand (coll. E. S. Gourlay) which are referable to this genus.

Included species. The following species have been examined and found to be referable to this genus:

Spolas citricincta (Ashmead), *S. delicata* (Ashmead), *S. flavifrons* (Ashmead), *S. haleakale* (Ashmead), *S. hawaiiensis* (Ashmead), *S. molokaiensis* (Ashmead), *S. tarsata* (Ashmead) and *S. tephrias* (Perkins). Two further undescribed species have been seen.

Genus *METOA* Townes

Metoa Townes, 1971 : 147. Type-species: *Anomalon exile* Provancher, 1874 : 175, by original designation.

Eyes without pubescence, margins ventrally convergent; occipital carina complete, medio-dorsally distant from posterior ocelli; frons without a median vertical carina. Antennae rather short to moderately long, those of ♀ without a white band; scape truncate, about 1·2 times as long as pedicel; fourth flagellar segment about 3·0 times as long as broad. Apex of clypeus convex or with two latero-median teeth; mandible bidentate, lower tooth distinctly the shorter, often very reduced to absent, apices not twisted; labial palpi of three segments. Genal carina joining hypostomal carina close to base of mandible.

Pronotum dorsally moderately long, subvertical, without transverse furrow, posterior corner not occluding spiracular sclerite; lower anterior margin of pronotum without a tooth, lower corner truncate. Anterior of mesoscutum evenly rounded, without a concavity; notaulus absent or indistinct; medio-posterior region of mesoscutum punctate; transverse suture of mesoscutum absent, transverse furrows absent. Epicnemial carina reaching above centre of mesopleuron, with upper end close to and parallel with anterior margin of mesopleuron; epicnemial carina medio-ventrally very weakly produced; sternaulus indistinct; posterior transverse carina of mesosternum complete.

Fore coxae smooth; fore tibial spur with numerous acute macrotrichia along inner face. Mid tibia with two apical spurs. Hind trochanter more than 2·0 times as long as trochantellus; hind tarsal claws weakly curved, rather long, pectinate to near apex.

Forewing with *Rs* weakly sinuate; *2 + 3rm* proximal to *2m–cu*; *1m–cu* and Cu_{1a} basally close together, but not touching. Hindwing with six hamuli on R_1; distal abscissa of Cu_1 absent.

CI = 0·10*; BI = 1·20*; DBI = 0·55*; MI = 1·90*; RI = 0·90*; PI = 1·65*; ICI = 1·25*.

Propodeum reticulate, spiracle less than 2·0 times as long as broad; posterior of propodeum reaching 0·4 of length of hind coxa. Gaster elongate.

♀ genitalia. Valvula 3 about as long as apical depth of abdomen; ovipositor with apex abruptly constricted, constricted part more than 3·0 times as long as median thickness of ovipositor, extreme apex decurved; ovipositor laterally compressed.

♂ genitalia. Single syntergum present although with anterior margin markedly indented centrally; ninth abdominal sternite transverse, truncate posteriorly; gonosquamae short, acute. Gonolaciniae abruptly rounded distally about 90°; teeth moderately large; apodeme straight, reaching 0·5 of length of basivolsellar strut. Distivolsella moderately broad basally, about 0·55 times as wide as long; clasping face flat, teeth arranged diagonally. Parameres proximally obliquely truncate. Aedeagus in profile almost straight, apically evenly rounded with dorsal and ventral membranous regions present; ventral membranous area large, laterally extended into two small triangular flanges (Text-fig. 139).

This genus is immediately distinguished by the shape of the head dorsally. The occipital carina is separated from the posterior ocelli by at least 3·0 times the ocellar diameter.

Distribution. This is a small genus only recorded from the Nearctic region.

Included species. Only one species, *M. exilis* (Provancher), is known to be

referable to this genus. A second species is represented by a damaged specimen in the collections of the BMNH.

Genus *CALCANEUM* Townes

Calcaneum Townes, 1971 : 145. Type-species: *Calcaneum oporinum* Townes, 1971 : 146, by original designation.

At present no further information may be added to the original description included by Townes.

Distribution. This genus in apparently restricted to the Nearctic region.

Included species. Only the type-species, *Calcaneum oporinum* Townes, is known to be referable to this genus.

Genus *CLATHA* Cameron

Clatha Cameron, 1905*a* : 129. Type-species: *Clatha longipes* Cameron, 1905*a* : 130, by monotypy.

Eyes glabrous, weakly convergent ventrally; occipital carina complete, mediodorsally often weakly concave, close to posterior ocelli; frons without a median vertical carina. Antennae long, those of ♀ without a white band, scape truncate, 1·5 times as long as pedicel, fourth flagellar segment 4·0 times as long as broad. Apex of clypeus with a median apical tooth; mandibles bidentate, lower tooth distinctly the shorter, apex twisted about 30°; labial palps with three segments. Genal carina joining hypostomal carina before base of mandible.

Pronotum dorsally moderately long, subvertical, flat, posterior corner occluding up to 0·5 of spiracular sclerite; lower anterior margin of pronotum with tubercle at base of epomia, lower corner truncate. Anterior of mesoscutum abruptly but evenly rounded, with a small apical concavity; notaulus indistinct or absent; medio-posterior region of mesoscutum punctate or coriaceous, transverse suture of mesoscutum present, transverse furrows absent. Epicnemial carina reaching to about 0·4 of way up mesopleuron, sinuate with upper end remote from anterior margin of mesopleuron; epicnemial carina medio-ventrally raised into an acute protruberance which projects towards fore coxae; sternaulus absent; posterior transverse carina of mesosternum complete.

Fore coxae smooth; fore tibial spur with numerous acute macrotrichia on inner face; mid tibia with two apical spurs; hind trochanter more than 2·0 times as long as trochantellus; hind tarsi of ♂ not explanate; hind tarsal claws short, curved, pectinate almost to apices, not obviously sexually dimorphic.

Forewing with *Rs* straight; 2 + 3*rm* proximal to 2*m–cu*; 1*m–cu* and Cu_{1a} basally united. Hindwing with 5–6 hamuli on R_1; distal abscissa of Cu_1 absent.

BI = 3·80–4·10*; DBI = 0·85–0·95*; MI = 2·60–2·85*; RI = 0·50–0·65*; ICI = 0·50–0·60*; PI = 3·20–3·52*.

Propodeum reticulate, spiracles more than 3·0 times as long as broad; propodeum posteriorly reaching about 0·5 of length of hind coxa. Gaster elongate.

♀ genitalia. Valvula 3 about 1·2 times as long as tergite 3; apex of ovipositor abruptly constricted, constricted part about 3·0 times as long as thickness of ovipositor medianly, extreme apex straight; ovipositor weakly laterally compressed; unusual in having dorsal subapical swelling conspicuously enlarged, very convex.

♂ genitalia. Single syntergum present; ninth abdominal sternite transverse, posteriorly truncate; gonosquamae moderate in length. Gonolaciniae very elongate and slender, distally angled about 20°; teeth large, arranged on swollen area; apodeme almost straight, reaching 0·9 of length of basivolsellar strut. Distivolsella moderately broad, distally tapered slightly,

basally about 0·65 times as wide as long; clasping face flat except for the bases of large spines that are clustered centrally. Paramere proximally spatulate. Aedeagus in profile more or less straight, apically acutely pointed with small dorsal and ventral membranous areas; lateral sclerotized region extending medio-apically well beyond membranous areas; ventral area not laterally extended (Text-figs 43, 53, 71, 134).

The form of the male claspers of species of this genus is quite unlike that of any other except *Atrometus*. The affinities of this genus are at present not clear but it is closely related to *Atrometus*. These genera do not appear to be particularly closely related to other 'Podogastrine' genera. The aedeagus is not unlike that of *Spolas* species.

Distribution. Oriental but possibly also occurs in East Africa.

Included species. Only one named species, *C. longipes* Cameron, is known but a second species is represented by two males in the collections of the BMNH.

Genus ***ATROMETUS*** Foerster

Atrometus Foerster, 1868 : 146. Type-species: *Atrometus insignis* Foerster, 1878 : 77, by subsequent designation (Viereck, 1914*a* : 17).

Eye glabrous, inner margins subparallel; occipital carina present, mediodorsally separated from posterior ocelli by about 1·0 times the ocellar diameter; frons without a median vertical carina. Antennae moderately long, scape truncate, about 1·2 times as long as pedicel; fourth flagellar segment about 2·0 times as long as broad. Clypeus with a median apical tooth; mandible bidentate, lower tooth distinctly the shorter, apices twisted about 30°; labial palpi with three segments, cardo basally lobate. Genal carina joining hypostomal carina at or before mandibular base.

Pronotum dorsally long, subvertical, without a transverse furrow, posterior corner occluding about 0·7 of spiracular sclerite; lower anterior margin of pronotum with a tubercle at the base of epomia, lower corner acute. Mesoscutum anteriorly abruptly rounded, without an apical concavity; notauli indistinct or weak; medio-posterior region of mesoscutum coriaceous; transverse suture of mesoscutum present, transverse furrows absent. Epicnemial carina reaching to centre of mesopleuron, parallel to anterior margin of mesopleuron; epicnemial carina medio-ventrally strongly produced into acute process that extends between anterior coxae; sternaulus absent; posterior transverse carina of mesosternum complete.

Fore coxa smooth; fore tibial spur with numerous acute macrotrichia on inner face. Mid tibia with two spurs. Hind trochanter 1·2 times as long as trochantellus; hind tarsi of male very swollen; hind tarsal claws curved, basally pectinate.

Forewing with *Rs* weakly bowed; $2 + 3rm$ proximal to $2m\text{–}cu$; $1m\text{–}cu$ and Cu_{1a} basally contiguous. Hindwing with 6–8 hamuli on R_1; distal abscissa of Cu_1 absent.

BI = 1·75–1·85*; DBI = 0·85–0·92*; MI = 1·90–2·00*; RI = 0·87–0·94*; ICI = 1·10–1·22*; PI = 2·60–2·80*.

Propodeum reticulate, spiracles more than 5·0 times as long as broad; propodeum posteriorly reaching about 0·5 of length of hind coxa. Gaster elongate.

♀ unknown.

♂ genitalia. Single syntergum present; ninth abdominal sternite rhomboidal; gonosquamae long, terminally acute. Gonolacinia very elongate and slender, distally angled about 30°; teeth large; apodeme almost straight, about 0·8 of length of basivolsellar strut. Distivolsellar slender, basally less than 0·2 times as wide as long; clasping face convex, large teeth centrally arranged. Paramere proximally spatulate-lobate. Aedeagus in profile decurved, terminally rounded, extreme apex weakly upcurved, separate dorsal and ventral membranous areas present; lateral sclerotized region apically bifid, lower branch reaching margin of aedeagus and protruding as an out-turned flap (Text-figs 34, 135).

The structure of the male genitalia is very similar to that of *Clatha* though less specialized. In both genera there is considerable modification of the claspers in a similar way and the structure of the aedeagus is also similar. It is considered likely that these two genera are very closely related.

Distribution. This genus is recorded from the Mediterranean region.

Included species. Only a single species, *A. insignis*, is known to be referable to this genus at present.

Genus ***CECHENODES*** Townes

Cechenodes Townes, 1971 : 150. Type-species: *Cechenodes oweni* Townes, 1971 : 151, by original designation.

Eye with scattered pubescence, margins ventrally convergent; occipital carina complete, mediodorsally arched weakly, close to posterior ocelli; frons with a median vertical carina. Antennae long, those of ♀ without a white band; scape truncate, about 1·2 times as long as pedicel; fourth flagellar segment about 3·0 times as long as broad. Clypeus with a median apical tooth; mandibles bidentate, lower tooth distinctly the shorter, apices twisted slightly; labial palpi with three segments. Genal carina joining base of mandible separated from hypostomal carina.

Pronotum dorsally very long, subvertical, with a transverse furrow; posterior corner almost entirely occluding spiracular sclerite; lower anterior margin of pronotum with a tubercle at base of epomia, lower corner truncate. Anterior of mesoscutum abruptly rounded, without concavity; notauli present anteriorly as rugose areas; medio-posterior region of mesoscutum rugose; transverse suture of mesoscutum present, transverse furrows absent. Epicnemial carina reaching above centre of mesopleuron, close to anterior mesopleural margin and with upper end reaching margin; epicnemial carina medio-ventrally very weakly raised into a flange; sternaulus absent; posterior transverse carina of mesosternum complete.

Fore coxae smooth; fore tibial spurs with numerous acute macrotrichia on inner face. Mid tibia with two spurs. Hind trochanter about 1·3 times as long as trochantellus; hind tarsal claws pectinate on basal 0·7.

Forewing with *Rs* sinuate; 2 + 3*rm* proximal to 2*m–cu*; 1*m–cu* and Cu_{1a} basally separated. Hindwing with 5–7 hamuli on R_1; distal abscissa of Cu_1 absent.

CI = 0·57–0·68*; BI = 2·00–2·15*; DBI = 0·65–0·76*; MI = 1·65–1·75*; RI = 0·85–0·97*; PI = 4·70–5·50*; ICI = 1·10–1·25*.

Propodeum reticulate, spiracle about 2·0 times as long as broad; propodeum posteriorly extended into an unsculptured neck about 1·4 times as long as hind coxae. Gaster elongate.

♀ genitalia. Valvula 3 about 0·55 times as long as tergite 3; apex of ovipositor constricted, the constricted part at least 3·0 times as long as thickness of ovipositor medianly; extreme apex weakly decurved; ovipositor weakly laterally compressed.

♂ genitalia. Single syntergum present; ninth abdominal sternite transverse, posteriorly truncate; gonosquamae short, truncate. Gonolaciniae distally rather abruptly curved about 85°; teeth large; apodeme straight, extending 0·5 of length of basivolsellar strut. Distivolsella moderately broad, about 0·55 times as wide basally as long; clasping face flat, teeth arranged diagonally. Aedeagal paramere proximally unusually broad, truncate. Aedeagus in profile strongly geniculate, apically truncate; dorsal and ventral membranous areas present, the latter large and separated from the lateral sclerotized region by an invaginated area; ventral area laterally weakly extended into small triangular flanges (Text-figs 63, 137).

Distribution. This genus is only recorded from the Ethiopian region.

Included species. Only the type-species, *Cechenodes oweni* Townes, is referable to this genus at present.

Genus *BIMENTUM* Townes

Bimentum Townes, 1971 : 151. Type-species: *Bimentum notatum* Townes, 1971 : 152, by original designation.

Eyes without pubescence, margins ventrally subparallel or weakly convergent; occipital carina complete, medio-dorsally separated from hind ocelli by about diameter of ocellus; frons with indistinct median vertical carina. Antennae very long, those of ♀ without a white band; scape truncate, about 1·2 times longer than pedicel; fourth flagellar segment about 3·0 times as long as broad. Clypeus with a median apical tooth; mandible bidentate, lower tooth a little shorter than upper, apices twisted about 40°; labial palps with three segments. Genal carina joining hypostomal carina away from base of mandible.

Pronotum dorsally long, subvertical, without a transverse furrow, posterior corner covering spiracular sclerite; lower anterior margin of pronotum with an indistinct tubercle at base of epomia, lower corner truncate. Anterior of mesoscutum very abruptly rounded, without an apical concavity; notauli impressed, not extending beyond centre of mesoscutum; medio-posterior region of mesoscutum punctate, transverse suture of mesoscutum present, transverse furrows absent. Epicnemial carina reaching to centre of mesopleuron, its upper end reaching anterior margin of mesopleuron and with lower region close to lower corner of pronotum; epicnemial carina medio-ventrally produced into a weak lamella; sternaulus absent; posterior transverse carina of mesosternum complete.

Fore coxae smooth; fore tibial spur with numerous acute macrotrichia along inner face. Mid tibia with two spurs. Hind trochanter about 2·0 times as long as trochantellus; hind tarsi of ♂ not swollen; hind tarsal claws curved, pectinate beyond centre; not obviously sexually dimorphic.

Forewing with *Rs* almost straight; 2 + 3*rm* proximal to *2m–cu*; 1*m–cu* and Cu_{1a} basally united. Hindwing with 8–9 hamuli on R_1; distal abscissa of Cu_1 absent.

BI = 2·30–2·50*; DBI = 0·90–1·05*; MI = 2·00–2·15*; RI = 1·05–1·20*; ICI = 1·20–1·40*; PI = 3·50–4·00*.

Propodeum reticulate, spiracle at least 5·0 times as long as broad; propodeum posteriorly extended into sculptured neck about 0·6 times as long as hind coxae. Gaster elongate.

♀ genitalia. Valvula 3 0·6–0·8 times as long as abdominal tergite 3; apex of ovipositor constricted, constricted part more than 3·0 times as long as thickness of ovipositor medianly, extreme apex weakly decurved; ovipositor weakly laterally compressed.

♂. Not available for dissection.

Townes includes *Podogaster spilopterus* within this genus but examination of the type-material of this species has shown that it is not congeneric with *B. notatum*. This species is very distinct from any other described genus and is placed in a separate new genus described below.

Distribution. Townes (1971; 1973) has recorded this genus only from the Ethiopian region but in the collections of the BMNH is a single female of an undescribed species from Madagascar.

Included species. Only one named species, *Bimentum notatum* Townes, is referred to this genus at present.

Genus *VERNAMALON* gen. n.

Type-species: *Podogaster spilopterus* Morley, 1913*a* : 61.

Eye without pubescence, margins ventrally moderately convergent; occipital carina complete, mediodorsally widely separated from posterior ocelli by more than 3·0 times ocellar diameter; frons with an indistinct median vertical carina. Antennae moderately long, those of ♀ without

a white band; scape truncate, 1·5 times longer than pedicel, in the male with the scape flattened on inner surface; fourth flagellar segment about 3·0 times as long as broad. Clypeus with a pair of median apical teeth; mandible bidentate, lower tooth a little shorter than upper; apices weakly twisted about 15°; labial palpi with three segments. Genal carina joining hypostomal carina away from mandible base.

Pronotum dorsally long, vertical, without a transverse furrow, posterior corner occluding about 0·5 of spiracular sclerite; lower anterior margin of pronotum without a tubercle, lower corner truncate. Anterior of mesoscutum rather evenly rounded with a shallow apical concavity; notauli represented by a shallowly coriaceous area which in posterior 0·5 of mesoscutum is produced into an obvious raised ridge (Text-fig. 231); medio-posterior region of mesoscutum rugose; transverse suture of mesoscutum present, transverse furrows absent. Epicnemial carina reaching to centre of mesopleuron, its upper end reaching anterior margin of mesopleuron; epicnemial carina medio-ventrally produced into weak lamella; sternaulus absent; posterior transverse carina of mesosternum complete.

Fore coxae smooth; fore tibial spur with numerous acute macrotrichia on inner face. Mid tibia with two spurs. Hind trochanter subequal in length to trochantellus; hind tarsi of ♂ not swollen; hind tarsal claw curved, basally pectinate, not obviously sexually dimorphic.

Forewing with vein *Rs* distally curved; 2 + 3*rm* proximal to 2*m–cu*; 1*m–cu* and Cu_{1a} basally contiguous. Hindwing with 6–8 hamuli on R_1; distal abscissa of Cu_1 absent.

BI = 1·28–1·35*; DBI = 0·65–0·75*; MI = 1·37–1·62*; RI = 0·90–1·05*; ICI = 0·90–1·12*; PI = 1·40–1·60*.

Propodeum reticulate with spiracle about 4·0 times as long as broad; propodeum posteriorly extended 0·5 of length of hind coxae. Gaster elongate.

♀ genitalia. Valvula 3 0·7 times as long as tergite 3; apex of ovipositor simply acutely pointed; extreme apex straight; ovipositor not at all laterally compressed.

♂ genitalia. Single syntergum present; ninth abdominal sternite transverse; posteriorly truncate; gonosquamae large, truncate, weakly sclerotized. Gonolaciniae distally evenly curved about 80°; teeth large; apodeme straight, extending 0·5 of length of basivolsellar strut. Distivolsella slender, basally 0·5 times as wide as long, apically acute; clasping face flat, teeth arranged peripherally. Aedeagal paramere proximally spatulate, pointed. Aedeagus in profile straight, apically rounded, very membranous; weakly sclerotized lateral area angled ventrally to reach apico-ventral corner of aedeagus; ventral region not laterally extended (Text-figs 48, 62, 66, 136).

This genus may be distinguished from *Bimentum* in the following ways: having the clypeus with a pair of apical teeth, having elaborate sculpture on the mesoscutum, having the hind trochanter subequal in length to the trochantellus, the form of the genitalia and having the occipital carina widely separated from the posterior ocelli.

The form of the clypeus and position of the occipital carina in this genus are similar to that of *Metoa* but *Metoa* lacks the transverse suture of the mesoscutum.

Distribution. This genus is only recorded from the Ethiopian region.

Included species. At present only the type-species, *Vernamalon spilopterum* (Morley), is referable to this genus.

Genus ***BRACHYNERVUS*** Uchida

Brachynervus Uchida, 1955 : 123. Type-species: *Brachynervus tsunekii* Uchida, 1955 : 124, by original designation.

Eyes glabrous, inner margins ventrally weakly convergent; occipital carina dorsally incomplete; frons with a raised lamella. Antennae very long, those of ♀ without a white band;

scape truncate, more than 2·0 times as long as pedicel; fourth flagellar segment about 1·5 times as long as broad. Clypeus with a pair of median teeth; mandibles bidentate, apices strongly twisted about 40°, angled, lower tooth a little shorter than upper; labial palps with three segments. Genal carina joining hypostomal carina before mandibular base.

Pronotum dorsally not long, vertical, without a transverse furrow, posterior corner not occluding spiracular sclerite, lower anterior margin of pronotum with a tooth, lower corner truncate. Mesoscutum anteriorly abruptly rounded without an apical concavity; notauli not discernible except as area of different coloration; medio-posterior region of mesoscutum reticulate; transverse suture of mesoscutum present, transverse furrows absent. Epicnemial carina laterally indistinct, medio-ventrally not raised; sternaulus indistinct; posterior tranverse carina of mesosternum absent.

Fore coxae with anterio-medial longitudinal carinae; fore tibial spur with numerous acute macrotrichia on inner face. Mid tibia with a single spur; hind trochanter about 1·8 times as long as trochantellus; hind tarsal claws geniculate with a basal lobe.

Forewing with *Rs* weakly sinuate; 2 + 3*rm* when present well proximal to 2*m–cu*, the veins separated by a length of *M* about equal in length to 2*m–cu* so that the second discal cell is approaching a regular pentagon in shape; 1*m–cu* and Cu_{1a} basally separated. Hindwing with seven widely spaced hamuli on vein R_1; distal abscissa of Cu_1 present.

CI = 0·51–0·56*; BI = 2·00–2·23*; DBI = 0·90–0·96*; MI = 2·00–2·20*; NI = 2·10–2·20*; RI = 1·20–1·30*; ICI = 0·15–0·19*; PI = 2·80–3·00*.

Propodeum reticulate, spiracle more than 7·0 times as long as wide; posterior of propodeum convexly rounded with insertion of petiolar segment well separated from insertion of hind coxae so that whole of propodeum appears globosely inflated. Gaster slender.

♀ genitalia. Valvula 3 about 0·6 times as long as tergite 3; ovipositor apically acute, without elongate tip, extreme apex straight; ovipositor markedly laterally compressed.

♂ genitalia. This was not available for dissection but the aedeagus of the type-specimen is described.

Aedeagus apically rounded, rather evenly sclerotized without distinct membranous areas and not laterally extended ventrally.

This is an extremely distinctive genus of doubtful affinity. Townes (1971) placed this genus in his Theriini but the wing venation, form of the propodeum and presence of the mesoscutal suture are characters not found in any other Theriine genera. The presence of the mesoscutal suture would seem to indicate that this genus is allied to the 'Podogastriine' genera but *Brachynervus* differs from these in having the distal abscissa of Cu_1 present in the hindwing and the posterior transverse carina of the mesosternum vestigial, as well as in the form of the wing venation and shape of the propodeum.

There is in the collection of the BMNH a species described as *Anomalon tinctipenne* Cameron by Morley (1913*a*). The type-specimen of *A. tinctipenne* (deposited at the University Museum, Oxford) is referable to the genus *Heteropelma* and is a different species. *A. tinctipenne* Cameron sensu Morley is a new species of *Brachynervus* and is described below.

Brachynervus confusus sp. n.

[*Anomalon tinctipenne* Cameron sensu Morley, 1913*a* : 83. Misidentification.]

Holotype ♀, China: Shantung, Ching-tao (Tsingtao) Lazarettgarten, August, no further date (*Hoffman*) (BMNH).

Forewing 13 mm.

Antennae very long, with 72 flagellar segments; lower face rather flat; cheeks broad, distance between orbit and mandibular base approximately the same as the length of second flagellar segment. Clypeus small, flat and apically with a median notch; mandibles short, at their distal end abruptly curved; lower tooth 0·5 of length of upper. Frons with a median vertical lamella; head in profile with gena centrally broad, narrowed dorsally and ventrally.

Scutellum deplanate; posterior transverse carina of mesosternum present vestigially only before each mid coxae; entire thorax and propodeum coarsely reticulately rugose. Fore and mid tarsal claws strongly curved, coarsely pectinate except apically, hind tarsal claws strongly geniculate, not pectinate.

Wings infumate. Head black; genae, marks on vertex, lower face, clypeus and mandibles, except apically, yellow; antennae fulvous, scape basally reddish brown, apically yellow. Thorax black, yellow-marked on anterior margin of pronotum, mesoscutum in four longitudinal stripes and entirely apically, tegulae, subalar prominance, scutellum, postscutellum, metanotum and propodeum apically and laterally. Fore and mid legs yellow, hind legs red brown with tarsi yellow. Abdomen concolorous red-brown.

♂ unknown.

Paratype. (Terminal segments of abdomen missing.) India: Khasia Hills, no further data (BMNH).

B. confusus differs from the type-species of the genus *B. tsunekii* principally in the wing venation. *B. tsunekii* has 2 + 3*rm* entirely lacking and the second discal cell almost regularly pentagonal. *B. confusus* has 2 + 3*rm* present and the second discal cell irregularly pentagonal (Text-figs 199, 200).

Distribution. This genus appears to be restricted to colder parts of the south-eastern Palaearctic region.

Included species. Only two species, *B. tsunekii* and *B. confusus*, are known to be referable to this genus.

Genus ***PODOGASTER*** Brullé

Podogaster Brullé 1846 : 179. Type-species: *Podogaster coarctata* Brullé, 1846 : 179, by monotypy.

Eye with sparse hair, margins exceptionally strongly convergent ventrally; occipital carina complete, sometimes dorsally indistinct, close to posterior ocelli; frons without a median vertical carina. Antennae long, those of ♀ without a white band; scape truncate to slightly oblique, 0·9–1·2 times as long as pedicel; fourth flagellar segment about 4·0 times as long as broad. Clypeus with a median apical tooth; mandibles bidentate, lower tooth distinctly the shorter, apically twisted about 30°; labial palpi with three segments; cardo basally lobate. Genal carina present or absent, when present joining hypostomal carina before mandible base.

Pronotum dorsally wide or moderately wide, subvertical, without a distinct continuous transverse furrow; posterior corner not or only just occluding spiracular sclerite; lower anterior margin of pronotum with a blunt tooth at base of epomia, lower corner truncate. Anterior of mesoscutum abruptly rounded, without an apical concavity; notauli impressed, coriaceously sculptured; medio-posterior region of mesoscutum rugose; transverse suture of mesoscutum present, transverse furrows absent. Epicnemial carina reaching above centre of mesopleuron, its upper end joining anterior margin of mesopleuron; epicnemial carina medio-ventrally produced into an acute process that is extended between the anterior coxae; sternaulus present, strongly impressed, 0·3–0·6 times as long as mesopleuron; posterior transverse carina of mesosternum complete.

Fore coxae smooth; fore tibial spur with numerous acute macrotrichia on inner face. Mid

tibia with two spurs. Hind trochanter 2·5 times as long as trochantellus; hind tarsi of ♂ not swollen; hind tarsal claws pectinate almost to apex, not obviously sexually dimorphic.

Forewings with *Rs* straight; 2 + 3*rm* proximal to 2*m–cu*; 1*m–cu* and Cu_{1a} basally adjacent; hindwing with 3–5 hamuli on R_1; distal abscissa of Cu_1 absent.

BI = 1·90–2·90; DBI = 1·25–1·42; MI = 2·35–3·10; RI = 1·00–1·15; ICI = 0·35–0·62; PI = 9·00–11·00.

Propodeum reticulate, spiracles about 2·5 times as long as broad; posterior of propodeum extended into a smooth 'neck' that is 0·95 of length of hind coxa. Gaster elongate.

♀ genitalia. Valvula 3 about 1·5 times as long as abdominal tergite 3; apex of ovipositor constricted, constricted part about 2·5 times as long as median thickness of ovipositor, extreme apex decurved; ovipositor weakly laterally compressed.

♂ genitalia. Single syntergum present or with medio-anterior dorsal membrane partially separating syntergites; gonosquamae short. Gonolaciniae distally evenly angled about 50°; teeth indistinct; apodeme angled about 10° from axis of gonolacinia, extending 0·65 of length of basivolsellar strut. Distivolsellar moderately broad, 0·65 times as broad basally as long; clasping face flat, teeth arranged peripherally. Aedeagal paramere proximally angled, lobate, elongately acute. Aedeagus in profile with apex weakly decurved, apically rounded, membranous; lateral sclerotized region not reaching apex of aedeagus, subterminally geniculate, terminally spinose and with a subterminal broad flattened region (Text-figs 78, 124).

The form of the aedeagus and claspers of this and the following genera are quite different from those of the Old World genera to which they were considered to be related. It is possible that these two genera may have evolved quite separately from the Old World 'Podogastrine' genera. This hypothesis is more fully discussed below.

Distribution. This genus is only recorded from the Neotropical region.

Included species. The following have been examined: *P. coarctata* Brullé, *P. striata* (Cameron) and four undescribed species.

Genus ***PHILODRYMUS*** Townes

Philodrymus Townes, 1971 : 153. Type-species: *Anomalon vitticolle* Cresson, 1874 : 377, by original designation.

Eye with few sparse hairs, margins strongly convergent ventrally; occipital carina complete, close to posterior ocelli; frons without a median vertical carina. Antennae long, those of ♀ without a white band; scape slightly oblique, about 1·0–1·2 times as long as pedicel; fourth flagellar segment about 4·0 times as long as broad. Clypeus with a median apical tooth; mandibles bidentate, apices twisted about 30°, lower tooth distinctly the shorter; labial palpi with three segments; cardo basally lobate. Genal carina present or absent, when present joining hypostomal carina before base of mandible.

Pronotum dorsally moderately long, subvertical, without a distinct transverse furrow, posterior corner not or slightly occluding spiracular sclerite; lower anterior margin of pronotum with a blunt tooth at base of epomia, lower corner truncate. Mesoscutum anteriorly abruptly rounded without an apical concavity; notauli impressed, coriaceous; medio-posterior region of mesoscutum rugose; transverse suture of mesoscutum present, transverse furrows absent. Epicnemial carina reaching above centre of mesopleuron, its upper end reaching anterior margin of mesopleuron; epicnemial carina medio-ventrally produced into an acute tooth which projects forward between bases of fore coxae; sternaulus present as an impressed region 0·3–0·6 times as long as mesopleuron; posterior transverse carina of mesosternum complete.

Fore coxae smooth, fore tibial spur with numerous acute macrotrichia along inner face. Mid tibia with two spurs. Hind trochanter about 2·5 times as long as trochantellus; hind

tarsi of ♂ not swollen; hind tarsal claws pectinate almost to apices, not obviously sexually dimorphic.

Forewing with *Rs* almost straight; 2 + 3*rm* proximal to 2*m–cu*; 1*m—cu* and Cu_{1a} basally contiguous; hindwing with 3–5 hamuli on vein R_1; distal abscissa of Cu_1 absent.

BI = 2·00–3·35; DBI = 1·10–1·65; MI = 2·00–3·40; RI = 1·00–1·60; ICI = 0·32–0·55; PI = 6·60–8·00.

Propodeum reticulate, spiracles about 2·5 times as long as broad; posterior of propodeum produced into a sculptured 'neck' that reaches about 0·6 of length of hind coxae, very rarely about 1·00 times as long as hind coxa. Gaster elongate.

♀ genitalia. Valvula 3 about 1·2 times as long as tergite 3; apex of ovipositor constricted, constricted part about 4·0 times as long as median thickness of ovipositor; extreme apex weakly decurved; ovipositor weakly laterally compressed (Text-figs 5, 27, 16).

♂ genitalia. Single syntergum present; ninth abdominal sternite transverse, posteriorly truncate; gonosquamae short, truncate. Gonolacinae distally abruptly curved about 50°; teeth minute; apodeme straight, about 0·5 times as long as basivolsellar strut. Distivolsella slender to moderately broad, basally 0·5–0·6 times as wide as long; clasping face very weakly convex, with transverse ridge bearing teeth. Aedeagal paramere proximally angled, lobate, elongately acute. Aedeagus in profile with apex weakly decurved, apically rounded, membranous; lateral sclerotized region not reaching to apex of aedeagus but subterminally geniculate, spinose, and immediately proximal to geniculation is a broadened flattened region (Text-figs 49, 61, 89, 125).

This genus is very similar, especially in the structure of the genitalia and in wing venation, to *Podogaster*. Only these two genera have the geniculate, partially flattened, apex of the lateral sclerotized aedeagal region. In both genera the distal ends of 1*A* in the forewing is well removed from the weak vannal notch and a small pigmented vein-like area is present extending from the distal end of 1*A* towards and distal to the vannal notch (Text-fig. 195). These genera are also somewhat unusual in having a very reduced number of hamuli on R_1. Even in species with a forewing length of 20 mm in many cases only three hamuli were observed to be present on R_1, whereas in most other genera, where species approach a similar size, there are usually twelve or more hamuli. The only exception to this is *Brachynervus* in which only six hamuli are present, but these are very widely separated, quite unlike those of any other genus.

Philodrymus may be distinguished from *Podogaster* not only in the shape of the propodeum (the character used by Townes) but also in having the eyes less strongly convergent ventrally, having the petiolar spiracles further from the posterior margin of the tergite, and having a shorter ovipositor with a more elongate tip.

Distribution. *Philodrymus* is only recorded from the Neotropical region.

Included species. The following species have been examined and found referable to this genus:

P. vitticollis (Cresson), *P. minor* (Szépligeti), *P. major* (Szépligeti) and four undescribed species.

Genus ***OPHIONELLUS*** Westwood

Pharsalia Cresson, 1872 : 177. Type-species: *Pharsalia texana* Cresson, 1872 : 177, by subsequent designation (Viereck, 1914*a* : 155). [Homonym of *Pharsalia* Thomson, 1864.]

Ophionellus Westwood, 1874 : 128. Type-species: *Ophionellus fragilis* Westwood, 1874 : 128, by monotypy.

Parophionellus Brues & Richardson, 1913 : 495. [Replacement name for *Pharsalia* Cresson.]
Hymenopharsalia Morley, 1913*a* : 97. [Replacement name for *Pharsalia* Cresson.]

Eye with elongate pubescence, inner margins ventrally strongly convergent; occipital carina close to hind ocelli, complete; frons without a median vertical carina. Antennae of moderate length, those of ♀ occasionally with a white band; scape truncate, 0·8 times as long as pedicel; fourth flagellar segment about 3·0 times as long as broad. Apex of clypeus rounded, truncate, or with median impression; mandibles bidentate, apices weakly twisted, lower tooth distinctly the shorter; labial palpi of three segments; cardo basally lobed. Genal carina joining base of mandible.

Pronotum dorsally long, flat, vertical; posterior corner not or partially occluding spiracular sclerite; lower anterior margin of pronotum with a tubercle at base of epomia; lower corner truncate. Mesoscutum anteriorly very angularly rounded, without a concavity; notauli indistinct; medio-posterior region of mesoscutum coriaceous; transverse suture of mesoscutum present, transverse furrows absent. Epicnemial carina reaching to centre of mesopleuron with upper end joining anterior margin of mesopleuron; epicnemial carina medio-ventrally produced into a weak process; sternauli represented by a flat glabrous area; posterior transverse carina of mesosternum complete.

Fore coxae smooth; fore tibial spur with a moderate number of subacuminate macrotrichia on inner face. Mid tibia with one spur. Hind trochanter more than 2·5 times as long as trochantellus; hind tarsi of ♂ not or weakly swollen; hind tarsal claws pectinate almost to apex, not obviously sexually dimorphic.

Forewing with *Rs* short, almost straight; 2 + 3*rm* distal to stub of ?2*m–cu*; 1*m–cu* and Cu_{1a} basally fused. Hindwing with 3–5 hamuli on R_1. Both wings with venation very reduced (Text-fig. 200).

MI = 2·30–2·60; PI = 1·40–1·70.

Propodeum weakly reticulate, spiracles less than 2·0 times as long as broad; posterior of propodeum reaching about 0·6 of length of hind coxae. Gaster exceptionally elongate and slender.

♀ genitalia. Valvula 3 a little longer than apical abdominal depth; apex of ovipositor evenly elongately acutely pointed, extreme apex weakly decurved; ovipositor laterally compressed; valvula 2 with numerous regular perforations (Text-fig. 25).

♂ genitalia. Single syntergum present; ninth abdominal sternite square, posteriorly truncate; gonosquamae elongately extended posteriorly. Gonolaciniae weakly curved about 40°; teeth minute; apodeme straight, 0·2 times as long as basivolsellar strut. Distivolsella broad, 1·0 times as broad as long; clasping face flat, teeth apico-peripherally arranged. Aedeagal paramere proximally acute. Aedeagus laterally weakly curved, apically rounded, dorsally rather uneven; whole of aedeagus rather evenly sclerotized; ergots conspicuous (Text-figs 93, 94, 126).

Ophionellus is one of the most easily distinguishable genera of Ichneumonidae on account of the extremely slender facies of these insects, which are only approached amongst Ichneumonids by some Cremastinae. Other characteristic features of this genus are the reduced venation (Text-fig. 200), the presence of silvery pubescence on the mesopleurae and the elongate gonosquamae of the male.

The female is unusual in having the second valvulae perforated, presumably to reduce weight.

The affinities of this genus are not known at present.

Distribution. This genus is mainly Neotropical with a few species in the southern Nearctic region.

Included species. The following species were examined and found to be referable to this genus:

O. fragilis Westwood, *O. texana* (Cresson) *O. albofacialis* (Cameron), *O. annulipes* (Cameron), *O. mexicanis* (Morley), *O. virginiensis* (Cresson) and three undescribed species.

Genus ***OPHIOPTERUS*** Brullé

Ophiopterus Brullé, 1846 : 153. Type-species: *Ophiopterus coarctatus* Brullé, 1846 : 153, by monotypy.
Ophionopterus Schultz, 1906 : 96. [Unjustified emendation.]
Ophionopterus Morley, 1912 : 66. [Unjustified emendation.]

Eye with short sparse pubescence or glabrous, inner margins ventrally convergent; occipital carina complete, medio-dorsally convex, close to posterior ocelli; frons without a median vertical carina. Antennae very elongate, those of ♀ with a white band; scape strongly oblique (Text-fig. 172); fourth flagellar segment about 4·0 times as long as broad. Apex of clypeus with a pair of teeth; mandibles bidentate, apices not twisted. lower tooth slightly shorter than upper; labial palps with three segments. Genal carina joining hypostomal carina before base of mandible.

Pronotum dorsally very long, flat, horizontal; posterior corner covering about 0·4 of spiracular sclerite; lower anterior margin with a tubercle at base of epomia; lower corner truncate. Mesoscutum anteriorly evenly rounded, without subapical concavity; notauli absent; medio-posterior region of mesoscutum punctate; transverse suture of mesoscutum present, transverse impressed furrows present. Epicnemial carina short, not reaching above lower 0·4 of mesopleuron and parallel to anterior margin of mesopleuron; epicnemial carina medio-ventrally produced into a large flange; sternaulus indistinct; posterior transverse carina of mesosternum complete.

Fore coxae smooth; fore tibial spur with numerous acute macrotrichia on inner face. Mid tibia with two spurs. Hind trochanter more than 2·0 times as long as trochantellus; hind tarsi of male not swollen; hind tarsal claws pectinate about 0·7 of length, not obviously sexually dimorphic.

Forewing with *Rs* very sinuate; 2 + 3*rm* distal to 2*m–cu*; 1*m–cu* and Cu_{1a} basally separated. Hindwing with 6–8 hamuli on R_1; distal abscissa of Cu_1 absent.

CI = 0·58–0·72*; BI = 1·70–1·83*; DBI = 0·85–0·91*; MI = 1·80–1·90*; RI = 1·20–1·35*; ICI = 0·85–0·90*; PI = 1·80–2·00*.

Propodeum reticulate, spiracle more than 2·0 times as long as broad; posterior of propodeum reaching 0·9 of length of hind coxae. Gaster elongate.

♀ genitalia. Valvula 3 as long as tergite 3; apex of ovipositor constricted, constricted part about 4·0 times as long as median thickness of ovipositor; extreme apex straight; ovipositor laterally compressed.

♂ genitalia. Single syntergum present; ninth abdominal sternite quadrate with anterior lateral corners produced (Text-fig. 42) posteriorly truncate; gonosquamae rather short. Gonolaciniae weakly curved distally evenly rounded about 50°; teeth minute; apodeme straight, 0·4 times as long as basivolsellar strut. Distivolsella of moderate width, about 0·55 times as broad basally as long; clasping face flat, teeth apico-peripherally arranged. Aedeagal parameres weakly sclerotized, proximally truncate. Aedeagus laterally almost straight, evenly sclerotized except for apical and ventral regions; entire apex of aedeagus membranous, rounded; ventral membranous region unclearly defined, not extended laterally, but with a median longitudinal fold (Text-fig. 138).

Distribution. This very distinctive genus is confined to the Neotropical and extreme southern Nearctic regions.

Included species. The following species were examined and found to be referable to this genus:

O. coarctatus Brullé, *O. cincticornis* (Cresson) and one undescribed species.

Tribe **ANOMALONINI** Viereck

Trachynotoidae Foerster, 1868 : 140. Type-genus: *Trachynotus* Gravenhorst (= *Anomalon* Panzer).
Trachynotina Foerster; Thomson, 1887 : 1048.
Trachynotini Foerster; Ashmead, 1894 : 277.
Nototrachini Ashmead, 1900 : 580. Type-genus: *Nototrachys* Marshall (= *Anomalon* Panzer).
Nototrachinae Ashmead; Dalla Torre, 1901 : 177.
Anomaloninae Viereck, 1918 : 72. Type-genus: *Anomalon* Panzer.
Anomalina Townes, 1945 : 708. [Homonym of Anomalitae Blanchard, 1851 : 173.]
Anomalonini Viereck; Hellén, 1950 : 31.
Anomalini Townes; Short, 1959 : 502.

For the diagnostic characters of the tribe see Table 3 (p. 93).

Although strict application of the Law of Priority would favour Trachynotini as the name of this tribe, I have followed all other recent authors in preferring the name Anomalonini. The corrected form Anomalini has not been adopted for the reasons given on p. 6.

Genus *ANOMALON* Panzer

Anomalon Panzer, 1804 : 115. Type-species: *Anomalon cruentatus* Panzer, 1804 : 115 [=*Ophion foliator* Fabricius, 1798 : 239], by monotypy.
Trachynotus Gravenhorst, 1829 : 713. Type-species: *Ophion foliator* Fabricius, 1798 : 239, by monotypy. [Homonym of *Trachynotus* Latreille, 1829.]
Nototrachys Marshall, 1872 : 259. [Replacement name for *Trachynotus* Gravenhorst.]
Ophiononeura Cameron, 1904 : 174. Type-species: *Ophiononeura flavomaculata* Cameron, 1904 : 175, by monotypy.
Stictophion Cameron, 1906 : 87. Type-species: *Stictophion rufipes* Cameron, 1906 : 86, by subsequent designation (Viereck, 1914*a* : 138).
Erythrophion Cameron, 1906 : 87. Type-species: *Erythrophion ferrugineus* Cameron, 1906 : 88 [= *Stictophion rufipes* Cameron, 1906 : 86], by monotypy.
Anomalum Schultz, 1906 : 96. [Unjustified emendation.]
Trachyopterus Morley, 1912 : 67. Type-species: *Trachyopterus primus* Morley, 1912 : 68, by monotypy.
Pseudonototrachys Meyer, 1930 : 221. Type-species: *Pseudonototrachys pallidus* Meyer, 1930 : 222 [= *Nototrachis* (sic) *kozlovi* Kokujev, 1915 : 537], by monotypy.
Microcremastus Hedwig, 1961 : 292. Type-species: *Microcremastus amseli* Hedwig, 1961 : 293, by subsequent designation (Townes, 1971 : 125).

Considerable confusion has existed over the use of the generic name *Anomalon* and this has resulted from misinterpretation of the original authorship.

Gravenhorst (1829) used *Anomalon* Jurine, 1807 to include all species now placed in the Therionini. Curtis (1828) designated *Ichneumon laetatorius* F. as the type-species of *Anomalon* Jurine, 1807, although this designation was apparently overlooked by all authors until Viereck (1914). Until the work of Townes *et al.* (1965), authors in western Europe still maintained the use of *Anomalon* Jurine in the Gravenhorstian sense, whilst using *Trachynotus* Gravenhorst for *Anomalon* Panzer, 1804. The argument proposed by Morice & Durrant (1914), suggesting that Curtis's original designation of *I. laetatorius* as the type-species of *Anomalon* Jurine, 1807 was invalid because this species was not included in the anonymous 'Erlangen

list' (sometimes attributed to Jurine, 1801), is itself now invalidated. This is because the 'Erlangen list' has been suppressed under the Plenary Powers for nomenclatural purposes by the International Commission on Zoological Nomenclature (Opinion 135, 1939). However the validity of Curtis's designation was questionable because *Anomalon* Jurine, 1807 is merely an interpretation of Panzer's earlier work (1804). In his discussion about *Anomalon*, Jurine includes a list of species that he considers are referable to this genus, cited in original combination. Amongst them he includes *Anomalon cruentatus* Panzer, the type-species of *Anomalon* Panzer, 1804. From this it may be deduced that Jurine was merely expanding Panzer's genus *Anomalon* (including within it all Ichneumonids without an areolet in the forewing) and not proposing a new genus. The designation of a type-species by Curtis may therefore be ignored as spurious since *Anomalon* Jurine, 1807 is not an available name.

Eye usually without pubescence, rarely with short sparse hairs; internal margins of eyes parallel or subparallel; occipital carina complete or centrally interrupted, far removed from posterior ocelli; frons with a median vertical carina. Antennae short, those of ♀ without a white band; scape moderately oblique, about 1·5 times as long as pedicel; flagellar segment 4 about 4·0 times as long as broad. Clypeus either apically rounded, or with a pair of median teeth, sometimes with lower face long so that distance from orbit to mandible base is more than 2·0 times the width of the mandible base; mandible bidentate, lower tooth varying from slightly smaller than upper to vestigial, rarely absent entirely; mandible apices not twisted; labial palps with three segments; cardo basally simple. Genal carina either reaching base of mandible or joining hypostomal carina.

Pronotum dorsally long, with anterior part horizontal and posterior part subvertical and therefore with a median transverse angulation; posterior corner of pronotum not occluding spiracular sclerite; lower anterior margin without a tooth, lower corner truncate. Mesoscutum steeply rounded anteriorly, without a concavity; notauli weak to strong; medio-posterior region of mesoscutum coriaceous; transverse suture of mesoscutum absent, transverse furrows absent. Epicnemial carina reaching above centre of mesopleuron, its upper end reaching anterior margin of mesopleuron; epicnemial carina medio-ventrally raised into a flange; sternauli usually absent, rarely impressed, but not reaching beyond centre of mesopleuron. Posterior transverse carina of mesosternum complete.

Fore coxae smooth; fore tibial spur with a moderate number of truncate macrotrichia along inner face. Mid tibia with a single apical spur. Hind trochanter more than 1·3 times as long as trochantellus; hind tarsi of ♂ not swollen; hind tarsal claws long, weakly curved, basally pectinate.

Forewing with *Rs* sinuate; 2 + 3*rm* distal to 2*m–cu*; 1*m–cu* and Cu_{1a} basally separated; unusual in having abscissa of Cu_1 between 1*m–cu* and Cu_{1a} angled at less than 35° to first abscissa of Cu_1. Hindwing with 5–11 hamuli on R_1; distal abscissa of Cu_1 absent.

CI = 0·55–0·62; BI = 1·25–1·45; DBI = 0·50–0·63; MI = 1·50–1·93; RI = 1·15–1·30; PI = 1·90–2·45; ICI = 0·80–1·10.

Propodeum weakly reticulate, in profile unusual in being convexly rounded and not posteriorly produced; spiracles about 3·0 times as long as broad. Gaster elongate, unusual in having tergite 3 with epipleuron separated by a longitudinal crease.

♀ genitalia. Valvula 3 from as long as tergite 3 to as long as gaster; apex of ovipositor elongately and simply acute, extreme apex not decurved; ovipositor not laterally compressed (Text-figs 4, 8, 22).

♂ genitalia. Single syntergum present; ninth abdominal sternite quadrate, posteriorly angularly rounded; gonosquamae short, obliquely truncate. Gonolaciniae distally evenly rounded about 45°; teeth absent; apodeme straight, extended about 0·6 of length of basivolsellar strut. Distivolsella slender, basally about 0·3 times as wide as long; clasping face flat,

teeth arranged periphero-diagonally. Aedeagal paramere proximally spatulate, truncate. Aedeagus in profile almost straight, apically rounded, dorsally concave so that there is an apico-dorsal prominence; aedeagus weakly and rather evenly sclerotized, apico-lateral region united medio-ventrally and produced proximally into a weak spine; lateral sclerotized region indistinctly defined apically; aedeagus not laterally extended (Text-figs 50, 67, 86).

Anomalon species are often very common in dry areas. Morphologically the species are very uniform except for some striking variations of a very few characters. The facial structure is particularly variable. The most extreme modification occurs in *A. rufipes* which has a very broad malar space with the face correspondingly elongate (Text-fig. 168) and the mandibles unidentate. Reduction of the lower mandibular tooth is an occurrence not uncommon amongst the Anomaloninae, as it has been observed to occur in many genera including *Anomalon*, *Habronyx* (*Austranomalon*), *Aubertiana*, *Atrometoides* and *Gravenhorstia* (*Erigorgus*). In the latter genera there is also reduction of the clypeus until, in extreme examples, the clypeal apex is concave. The functional significance of these modifications is not clear but it is noteworthy that this modification is most apparent in species of arid regions, *A. unidentator* and *Atrometoides winkleri* of the North Sahara, *Anomalon rufipes* of the Kalahari, *H.* (*Austranomalon*) from central Australia and *G.* (*Erigorgus*) *nigrita* from the Sonoran regions. Undoubedly one of the most important physical factors affecting insect distribution is the availability of water. It is considered possible that these modifications of the mouthparts may enable the Ichneumonids to obtain moisture from a source not available to those with the more normal mouthparts (that is shorter bidentate mandibles and large, centrally pointed clypeus). *A. rufipes* is also characterized by the swollen tibiae, which on the outer and posterior surfaces bear numerous flattened macrotrichia. These two obvious differences make *A. rufipes* a very distinct species but it does not justify the retention of a separate genus, *Stictophion*, as examination of a number of related species has revealed a continuous series of variation in the shape of the face and tibia, from the *Anomalon foliator*-type (Text-fig. 169) (short malar space and tibiae not swollen) to *A. rufipes*.

The wing venation is usually very constant throughout this genus but one New Guinea species, *A. taparilense*, entirely lacks vein *2m–cu*.

The final instar larvae of this genus are unusual in having mandibles bearing teeth.

The species of this genus are recorded as parasites of the larvae of Tenebrionidae.

Distribution. This is a cosmopolitan genus with species most numerous in drier regions.

Included species. The following species were examined and found to be referable to this genus:

A. foliator (F.), *A. australense* (Morley), *A. californicum* (Cresson), *A. formosanum* (Uchida), *A. frontale* (Cushman), *A. novoguineense* (Szépligeti), *A. variistriatum* (Morley), *A. ejuncidum* Say, *A. fuscipes* (Cameron), *A. primum* (Morley), *A. sinuatum* (Morley), *A. striatifrons* (Morley), *A. taparilense* Cheesman, *A. flavomaculatum* (Cameron), *A. nirvanum* (Morley), *A. rufipes* (Cameron), *A. tisisthenes* (Morley) and a large number of undescribed species.

Genus *NEOGREENIA* Viereck

Neogreenia Viereck, 1912*a* : 641. Type-species: *Neogreenia picticornis* Viereck, 1912*a* : 642, by original designation.

Eye surface with a few scattered hairs, inner margins weakly to moderately convergent ventrally; occipital carina usually broadly interrupted centrally, sometimes absent, remote from posterior ocelli; frons with or without a median vertical carina. Antennae short, those of ♀ usually with a white band; scape truncate, about 1·2 times as long as pedicel; fourth flagellar segment about 4·5 times as long as broad. Clypeus apically rounded or with a pair of median teeth; mandible bidentate, lower tooth distinctly the shorter; mandibular apices not twisted; labial palps with three segments. Genal carina meeting hypostomal carina near base of mandible.

Pronotum dorsally moderately long, subvertical, with a transverse furrow; posterior corner of pronotum not occluding spiracular sclerite; lower anterior margin without a tooth, lower corner truncate. Mesoscutum anteriorly abruptly rounded, without a concavity; notauli impressed, usually reaching beyond centre of mesoscutum; medio-posterior region of mesoscutum punctate to rugose; transverse suture of mesoscutum absent, transverse furrows absent. Epicnemial carina strong, reaching anterior margin of mesopleuron above the centre of the mesopleuron; epicnemial carina medio-ventrally raised into a flange; sternaulus distinct, extending more than 0·4 of length of mesopleuron. Posterior transverse carina of mesosternum complete.

Fore coxae smooth; fore tibial spur with many subacute macrotrichia on inner face. Mid tibia with a single spur. Hind trochanter more than 2·0 times as long as trochantellus; hind tarsi of ♂ not swollen; hind tarsal claws short, curved, basally pectinate.

Forewing with *Rs* almost straight to sinuate; 2 + 3*rm* absent or very short, when present distal to 2*m–cu*; 1*m–cu* and Cu_{1a} basally separated. Hindwing with 3–5 hamuli on R_1; distal abscissa of Cu_1 absent.

CI = 0·10–0·25; BI = 1·10–1·25; DBI = 0·55–0·64; MI = 1·70–2·35; RI = 0·30–0·40; PI = 1·30–1·52; ICI = 0·2–.

Propodeum reticulate; spiracle more than 3·0 times as long as broad; posterior of propodeum reaching about 0·1 of length of hind coxae. Gaster elongate, tergite 3 with epipleuron separated by a crease.

♀ genitalia. Valvula 3 about 1·3–1·6 times as long as tergite 3; ovipositor apically simply elongately acute, extreme apex not decurved; ovipositor weakly laterally compressed.

♂ genitalia. Very similar to *Anomalon* but with aedeagus apically membranous, rounded and without posteriorly directed ventral sclerotized process.

This genus is undoubtedly very closely related to *Anomalon* and Townes (1971 : 124) is of the opinion that *Neogreenia* is hardly more than a distinct species-group. In addition to the differences noted by Townes, *Neogreenia* differs from *Anomalon* in the value of RI and in lacking the ventral aedeagal process. It has therefore been decided to retain *Neogreenia* as a distinct genus.

Distribution. This genus is restricted to the New World.

Included species. The following species have been examined and found to be referable to this genus:

N. picticornis Viereck, *N. concolor* (Szépligeti), *N. levipectus* (Enderlein), *N. minima* (Ashmead) and also two undescribed species from South America.

INTERGENERIC RELATIONSHIPS

As a result of the detailed study of the morphology of the Anomaloninae, the results of which have been included above, it is possible to examine critically inter-

generic relationships, such as the suprageneric classification, and to propose a possible evolutionary scheme for the group.

Possible evolutionary interrelationships

Very few fossil species of Anomaloninae have been described. Brues (1910) described a number of species referable to four genera, *Gravenhorstia* (*Anomalon* sensu Gravenhorst), *Barylypa*, *Therion* and *Hiatensor*. The latter genus is known only from two fossil species. Because of this rarity of fossil material any attempt to assess evolutionary interrelationships must be almost entirely based on comparative morphology of modern species. Unlike the phenetic investigation described below, a phylogenic investigation relies on the selection of certain characters as being of greater evolutionary importance than others, and it is in this selection of characters that the greatest errors in a proposed system of phylogeny may be created.

Certain features amongst the Anomaloninae may be considered to be more primitive characters. Townes (1969) characterized the Anomaloninae by the complete absence in the final instar larva of the hypostomal spur. This observation has been found to be correct for the majority of Anomaloninae examined. However, *Habronyx* subgenus *Habronyx* species have been found to have a vestigial hypostomal spur. Presence of this spur may be considered as a primitive condition.

The majority of Ichneumonidae have the bases of veins Cu_{1a} and *1m-cu* of the forewing separate, although there is a tendency amongst some Anomaloninae to have these veins basally fused. Separation of these veins basally may be regarded as a less advanced condition. In more primitive Hymenoptera there is usually a large number of hamuli on vein R_1 of the hind wing. Loss of hamuli can be considered to be a more advanced feature. Likewise the reduction of the lower mandibular tooth and the number of palpar segments may be regarded as derived features, although there is no evidence to suggest that such atrophication has occurred only once in the evolution of the Anomaloninae.

Considering these features together it appears that the group of genera *Habronyx*, *Gravenhorstia* and *Aphanistes* are the most primitive and this deduction is supported by the little available fossil evidence. Interpretation of the evidence for the interrelationship of these genera is not easy and often evidence is somewhat ambiguous, but a tentative scheme of interrelationship is shown in Text-fig. 250. Amongst the more primitive Anomaloninae there has been two evolutionary pathways. One pathway has involved specialization of the egg development, of the lobed cardo and loss of the sexually dimorphic claws. Notauli have been retained. Near the base of this line of evolution must be *Habronyx heros* which maintains the reduced hypostomal spurs in the larval stage. This species is clearly related to the other *Habronyx* (*Habronyx*) species which show progressive enlargement of the dorsal area of the aedeagus, simplification of the tarsal claws and reduction of the length of the propodeum. There is some tendency within this group for an increase in the value of BDI.

Probably the primitive Tasmanian *Heteropelma* species, *Heteropelma flavitarse*

(which lacks the geniculate tarsal claws), is related to this evolutionary sequence. This line of development shows the retention of the specialized egg form, retention of the slender apically swollen distivolsella and retention of the broad larval pleurostoma as well as an increase in the development of a pronotal tooth and reduction of the membranous areas of the aedeagus. *H. flavitarse* is clearly related to *H. scaposum* but the latter has strongly geniculate hind tarsal claws. There are two apparent lines of evolution within *Heteropelma*. One shows increasing modification of the hind tarsi but retains the simply rounded clypeus whilst the other shows elaboration of the apico-clypeal region. *H. perornatum* is a rather specialized offshoot of the former which exhibits reduction in the size of the head and atrophication of the tibial spurs.

Another evolutionary interrelationship is that between *H. heros* and *H.* (*Camposcopus*) *nigricornis*. This sequence shows reduction of the cephalic capsule of the larva and a decrease in values of CI and TI. The relationship of these with *H.* (*Habrocampulum*) is not clear.

Aphanistes is related to the *Habronyx* species but has lost the caudal stalk of the egg though retaining the equatorial sucker (Text-fig. 99). This group shows progressive reduction in the size of the apico-dorsal membranous region of the aedeagus but exhibits stability in the positioning of $2 + 3rm$ and the structure of the mouthparts.

The other major evolutionary sequence has not involved specialization of the egg or cardo but has retained the sexually dimorphic claws and shows reduction of the notauli. The aedeagus of this group shows a tendency to develop an increasingly large apical lobe. This group retains a tendency for variation in the mouthparts and position of $2 + 3rm$ to occur.

Habronyx (*Austranomalon*) is an offshoot of this line but retains notauli. The remaining groups have completely lost the notauli. The interrelationship of the other subgenera can clearly be observed (Text-fig. 250).

The relationship of *Barylypa*/*Corsoncus* with the other genera is not particularly clear but it is possibly most closely related to *Habronyx* (*Austranomalon*). There are similarities between these two groups including the reduction of notauli, loss of apical clypeal tooth in some species, the decrease in value of CI and the lack of a strongly curved hypostoma in the larvae.

A relationship not shown in the figure is that of the above mentioned genera to *Therion* and *Trichomma*. These genera are clearly related to the *Habronyx*/*Heteropelma* line of evolution in retaining a specialized egg, large pleurostoma etc. They differ in having dissimilar aedeagi. However, *Therion*, *Trichomma*, *Heteropelma* and *Tanypelma* all have the gonolacinial apodeme formed from a sclerotized part of the outer margin of the gonolacinia (Text-figs 52, 55, 56, 57) and have similarly positioned teeth although these teeth are reduced to ridges in the genera *Trichomma* and *Tanypelma*. Despite the similarities between these genera it is evident that whilst *Tanypelma* and *Heteropelma* are very closely related, *Trichomma* and *Therion* have been evolving separately from the other two for a considerable time (Brues, 1910).

The position of the remainder of the genera in relation to those discussed is not

clear. Although *Agrypon* is superficially similar to *Barylypa*, there are marked differences in the form of the genitalia and cephalic capsule of the final instar larva. A few species of *Agrypon* (*A. clandestinum* for example) have a specialized egg indicating that, unlike *Barylypa*, species of this group are probably related to the *Habronyx* stock.

The interrelationship between the 'Podogastrine' genera is not clearly understood at present. *Clatha* and *Atrometus* have similarly modified claspers and are undoubtedly closely interrelated. Both these genera are unusual in having the gonolaciniar apodeme joining the inner edge of the gonolacinia and having the outer edge free (Text-figs 34, 53, 54, 58). This condition is also found in the genera *Parania* and *Spolas*. In all other 'Podogastrine' genera the gonolacinial apodeme is attached broadly to the entire base of the gonolacinia. The positioning of the gonolacinial teeth is similar in the genera *Clatha*, *Atrometus*, *Parania* and to a lesser extent *Spolas* which has rather small teeth. The positioning of the distivolsellar teeth is quite different in the latter genus. These four genera also have somewhat similar aedeagi. It is suggested that there may be a closer phylogenic relationship between these four genera than there is between *Clatha* and *Atrometus* and the other 'Podogastrine' genera. The remaining genera all have the aedeagal apices weakly convex and in the genera *Cechenodes*, *Vernamalon* and *Brachynervus* the ventral area is weakly expanded laterally into triangular flanges. The gonolacinia of *Vernamalon* and *Cechenodes* are similar in having a sclerotized process near the base of the gonolacinial apodeme.

Podogaster and *Philodrymus* are very closely related genera but the affinity between them and the Old World genera is not at all clear. There are several very obvious differences between the two groups, including the shape of the aedeagus, structure of the claspers, the number of hamuli, the form of the ovipositor apex and the development of sternauli. It is possible that the Neotropical genera are not as closely related to the Old Word genera as has been implied by including them together within a single tribe. The mesoscutal suture may have arisen independently within several different evolutionary lines. Until the species are better collected and more extensively studied little progress can be made in this sphere of investigation.

Suprageneric classification

The most recent system of classification of the Anomaloninae is that of Townes (1971) who divides the subfamily into four tribes, the Anomal[on]ini, Theriini, Podogastrini and Gravenhorstiini. Of these tribes only the Anomalonini have been found to be a distinct group.

The Anomalonini have been separated from the remainder (collectively called the Therionini) because of a number of differences. Several of these differences, though widely used, have been invalidated as a result of more recent work. The features by which the Anomalonini differ from the Therionini are given in Table 3.

Some of the morphological differences may be due to the dissimilar biologies of the Anomalonini and Therionini. The former are parasites of the larvae of

Coleoptera, especially Tenebrionidae, whereas the latter are parasites of lepidopterous larvae. Considering the combination of features of the Anomalonini as a whole it is evident that although they are similar in some respects to the Therionini, they represent a distinct and quite separate tribe. The present system of classification, that is to accord the Anomalonini, Theriini, Podogastrini and Gravenhorstiini equivalent taxonomic rank, does not accurately represent the phylogeny of the group as a whole. It can be deduced from the dendrogram (Text-fig. 249) and from Table 3 that the latter three tribes are more closely interrelated than any one is to the Anomalonini. It is therefore suggested that the groups Theriini, Gravenhorstiini and Podogastrini should all be included within a single tribe, the Therionini and that the Anomaloninae be composed of the two tribes Anomalonini and Therionini.

It can be seen from the dendrogram that the separation of the groups Theriini, Podogastrini and Gravenhorstiini within the Therionini is not at all clear. The Therionini divides initially into two groups at the 69 percentage similarity coefficient. One group contains thirteen genera, including part of the Theriini (that is *Therion*, *Heteropelma* and *Tanypelma*) and the majority of Gravenhorstiine genera but none of the Podogastrini. The second group contains fourteen genera and includes all of the Podogastrine genera and a few of the Gravenhorstiine genera (*Spolas*, *Metoa*, *Perisphincter*, *Phaenolabrorychus*, *Agrypon* and *Parania*).

Further examination shows that the first group divides into four subgroups before the 77 percentage similarity coefficient. One of these subgroups contains a single genus *Trichomma*, a second contains the Theriine genera (excluding *Brachynervus*), a third contains the genera *Clypeocampulum* and *Encardia*, while a fourth contains the majority of Gravenhorstiine genera. The second major group contains a less closely interrelated group of genera which show less tendency to cluster into subgroups which divide before the 77 percentage similarity coefficient into four. Two of these subgroups each contain a single genus, *Ophiopterus* and *Ophionellus* respectively, a third subgroup contains two genera, *Podogaster* and *Philodrymus*, and the fourth contains the remaining genera including all the 'Gravenhorstiine' genera placed in the group and the Old World 'Podogastrine' genera. More conventional examination of specimens has shown that the limits of the Theriini, Podogastrini and Gravenhorstiini are not easily definible and it is suggested that the system of dividing the Therionini into three groups should not be employed as it does not accurately represent the phylogeny of the group as a whole when all available evidence is considered.

Systematic position of the subfamily

There is considerable controversy over the systematic position of the Anomaloninae. Two interpretations are prevalent. Townes and co-workers (1961; 1965; 1966; 1969; 1971; 1973), basing their interpretation on the evidence of Short (1959), place the Anomaloninae adjacent to the Metopiinae. The second interpretation, that of the majority of European workers, Perkins (1959), Aubert (1966) and Viktorov (1968), retains the Anomaloninae within the Ophioninae.

TABLE 3

Comparison of the Anomalonini and Therionini

ANOMALONINI	THERIONINI
Valvula three longer than third tergite; valvifer two without dorsal apodeme.	Valvula three usually shorter than third tergite; valvifer two with a dorsal apodeme.
Clypeus rounded or bilobate.	Clypeus usually with a median point, rarely rounded, truncate, concave or bilobate.
Final instar larvae with mandibles with several teeth; parasitic upon coleopterous larvae.	Final instar larvae with mandibles simple; parasitic upon lepidopterous larvae.
Nervellus never intercepted and mid tibia unicalcarate.	Nervellus often intercepted and mid tibia, except in few rare genera, bicalcarate.
Propodeum only slightly extended beyond insertion of hind coxae.	Propodeum usually markedly extended beyond insertion of hind coxae.
Epipleuron of tergite three separated by a longitudinal crease.	Epipleuron of tergite three not separated by a longitudinal crease.

Short noted that the cephalic capsules of the final instar larvae of Anomaloninae are very similar to those of some Metopiinae. Both are similar in having large mandibles, a complete epistomal arch (not in some *Triclistus* species) and lack a hypostomal spur (with at the most a vestige present in *Habronyx* and *Gravenhorstia*). This similarity is the basis of the Townes interpretation of the position of the Anomaloninae. Reduction of the hypostomal spur has been observed in other subfamilies, notably the Ichneumoninae, Orthopelmatinae and Collyriinae. The loss of hypostomal spur can be correlated with the habits of the final instar larvae. Those which construct cocoons invariably have a well developed hypostomal spur whereas those that pupate in the host puparium, spinning only a flimsy cocoon, have the hypostomal spur reduced or absent.

The adult Anomaloninae are morphologically distinct from the Metopiinae. The former have the clypeus separated from the face by a distinct impression, have the petiole slender with the spiracles near the posterior margin, have all trochantelli differentiated, have the gaster compressed and usually have a subapical notch present on the ovipositor. The latter have the clypeus and face confluent, have the petiole broad with the spiracles at or anterior to the centre, do not have the fore and mid trochantelli differentiated and usually lack a subapical notch on the ovipositor. It is possible that the striking differences between adult Metopiinae and Anomaloninae may have resulted from dissimilarities in biology. The Metopiinae are adapted to mimic some Aculeates (*Metopius* for example mimics Eumenine wasps) whereas the bodies of most Anomaloninae are modified for concealment. Specimens of

Heteropelma calcator resting on conifers are very difficult to see. These differences in form are emphasized by behavioural differences. When taken in a sweep net, Metopiines buzz aggressively but Anomalonines usually remain motionless, often grasping a conifer twig and elevating the slender gaster at an angle approximately the same as that subtended by the leaves on the twig. Some species of *Gravenhorstia* are brightly coloured wasp mimics, but these species are not as slender as the majority of Anomaloninae, they are nonetheless quite unlike Metopiinae in body form.

The adult Anomaloninae are morphologically similar to the Ophioninae in a number of ways, such as the abdominal shape, form of the ovipositor and structure of the male genitalia. This similarity is the basis of the argument to retain the Anomaloninae within the Ophioninae. The cephalic capsules of the final instar larvae of Ophioninae differ considerably from those of the Anomaloninae in having an incomplete epistomal arch, minute mandibles and well developed hypostomal spurs. Unlike the Anomaloninae the Ophioninae complete their development outside the host pupa in a thick cocoon which the larva spins. Such a difference in biology could be the reason why the final instar larvae of the two groups are so dissimilar.

Little is known about the structure of the first instar larvae of any group of Ichneumonidae. Members of all three subfamilies (except for the Anomalonini) are recorded as parasites of similar ranges of lepidopterous hosts. In the majority of species the first instar larva lives within the haemocoel of the host. If there were a phylogenic affinity between any of the subfamilies it might be reasonable to suppose that there would be similarities between the first instar larvae. The first instar larvae of Metopiinae are quite different from those of the Anomaloninae or Ophioninae in having sharp L-shaped mandibles and lacking a caudal appendage (Gerig, 1960). The larvae of Anomaloninae and Ophioninae (and also some other subfamilies formerly included within the Ophioninae, the Porizontinae and Cremastinae) are characterized by an elongate caudal appendage (Plotnikov, 1914). The mandibles of the first instar larvae of Anomaloninae resemble the Ophioninae and Porizontinae in having large basal condyles but are distinct in having only a very short blunt tooth.

From the evidence presented above it can be concluded that the Anomaloninae are not related to the Metopiinae and that the similarity in the structure of the final instar larval head capsule is the result of evolutionary convergence. The Anomaloninae show some similarities to the Ophioninae and other subfamilies previously included within this subfamily and these similarities may be considered to indicate phylogenic affinity between the groups. However, as the Anomaloninae are distinct from the Ophioninae in a number of ways (Table 4) it is suggested that they should be retained as a separate subfamily but placed adjacent to the Ophioninae and Porizontinae.

UNPLACED SPECIMENS

During the preceding work it was not possible to place all specimens examined into the defined genera. The two unplaced specimens are considered to belong

Table 4

A comparison of some critical features of the subfamilies Metopiinae, Anomaloninae and Ophioninae

METOPIINAE	ANOMALONINAE	OPHIONINAE
Gaster dorso-ventrally flattened, first tergite broad, not elongate, with a pair of longitudinal carinae.	Gaster laterally compressed, first tergite elongate, simple and with spiracles near posterior margin.	Gaster laterally compressed, first tergite elongate, simple and with spiracles behind the centre.
Fore and mid legs with a single trochanteral segment.	All legs with two trochanteral segments.	All legs with two trochanteral segments.
Propodeum regularly carinate, with area superomedia distinct; posteriorly not extended far beyond insertion of hind coxae.	Propodeum irregularly carinate or reticulate, area superomedia not clearly defined; extended posteriorly into a neck beyond the insertion of the hind coxae.	Propodeum regularly or incompletely carinate, area superomedia present or absent; posteriorly extended but a little beyond the insertion of hind coxae.
Ovipositor without an apical constriction or subterminal notch.	Ovipositor apically constricted, usually with a subterminal notch.	Ovipositor not apically constricted but with a subterminal notch.
Wings large; forewing without an extra vein between vannal notch and tornus, disco-submarginal cell with evenly distributed microtrichia; anterior distal corner of first subdiscal cell with Cu_1 angled at emission of *1m–cu* at 130° or less.	Wings small, often with wingspan less than body length; forewing without an extra vein; discosubmarginal cell with evenly distributed microtrichia; anterior distal corner of first subdiscal cell with Cu_1 angled at emission of *1m–cu* at 125° or less.	Wings very large; forewing with an extra vein extending from the vannal notch to tornus; discosubmarginal cell with glabrous areas; anterior distal corner of first subdiscal cell with Cu_1 angled at emission of *1m–cu* at 145° or more.
Penis valve simple, elongately saggitate, without membranous region and with ergots quadrate.	Penis valve lobulate, explanate, with membranous regions and with ergots triangular.	Penis valve simple, elongate, terminally rounded, without a membranous region and with ergots triangular.
Ventral area of basivolsella membranous; distivolsella discrete, with small bipartite apodeme; basivolsellar strut large, sclerotized; gonolacinia weakly curved, terminally dentate.	Ventral area of basivolsella sclerotized, fused to distivolsella; distivolsellar apodeme conspicuous; basivolsellar strut weak; gonolacinia usually markedly curved, distally weakly dentate.	Ventral area of basivolsella somewhat sclerotized, fused to distivolsella; distivolsellar apodeme reduced; basivolsellar strut weak; gonolacinia strongly curved and elongately pointed.
Egg not exceptionally small, 0·3–0·9 mm long; final instar larvae with epistomal arch complete, hypostomal spur absent, mandibles large and pointed; completes development in host pupa, forms only thin cocoon.	Egg very small, 0·20–0·45 mm long; final instar larvae with epistomal arch complete, hypostomal spur vestigial or absent, mandibles large and pointed; completes development in host pupa, forms only thin cocoon.	Egg not small, 1·2–1·8 mm long; final instar larva with incomplete epistomal arch, hypostomal spur present, mandibles reduced in size; completes development in thick cocoon, typically pale banded.

to undescribed genera, but as in each case only a single specimen is known nothing further has been done other than to note their existence.

Species A. St. Helena: Knollcombes, 16.x.1959 (*C. R. Wallace*), BMNH. 1 ♂ similar to *Trichomma* species except that pubescence of eye is very short, clypeus is apically truncate, mandibular teeth are equal in length, propodeal spiracle is circular, scutellum is very convex and tarsal claws are short with large sparse pectinations extending to apex.

Species B. Pahang: Cameron Highlands, 1.ii.1968 (*C. G. Roche*), BMNH. 1 ♀ similar to *Agrypon* species with fore coxae without carinae, with mesoscutum with a transverse suture, and clypeus apically angled with a median apical tooth This species is exceptional in having large tentorial pits, which have a diameter exceeding the breadth of the malar space, and in having the ovipositor decurved, elongately and evenly tapered and without a trace of a dorsal notch so that the organ appears in side view, not unlike a sailmaker's needle.

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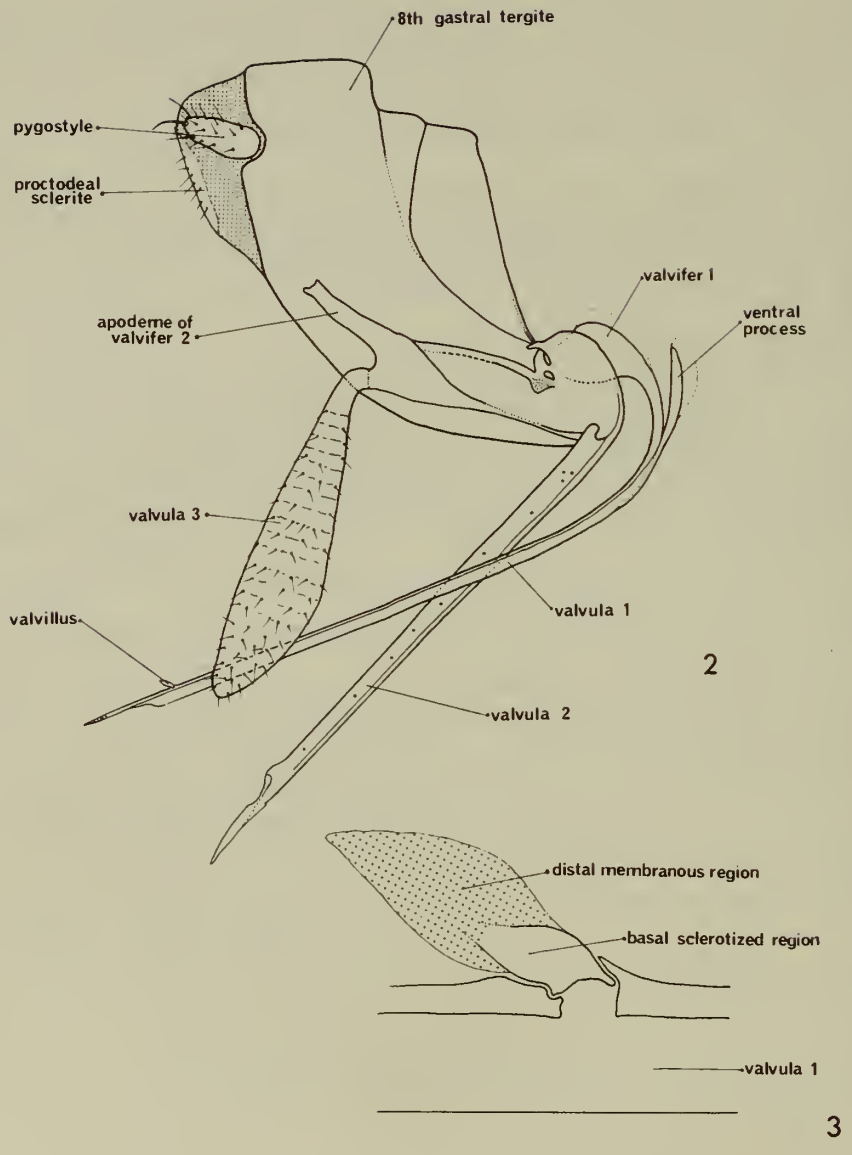
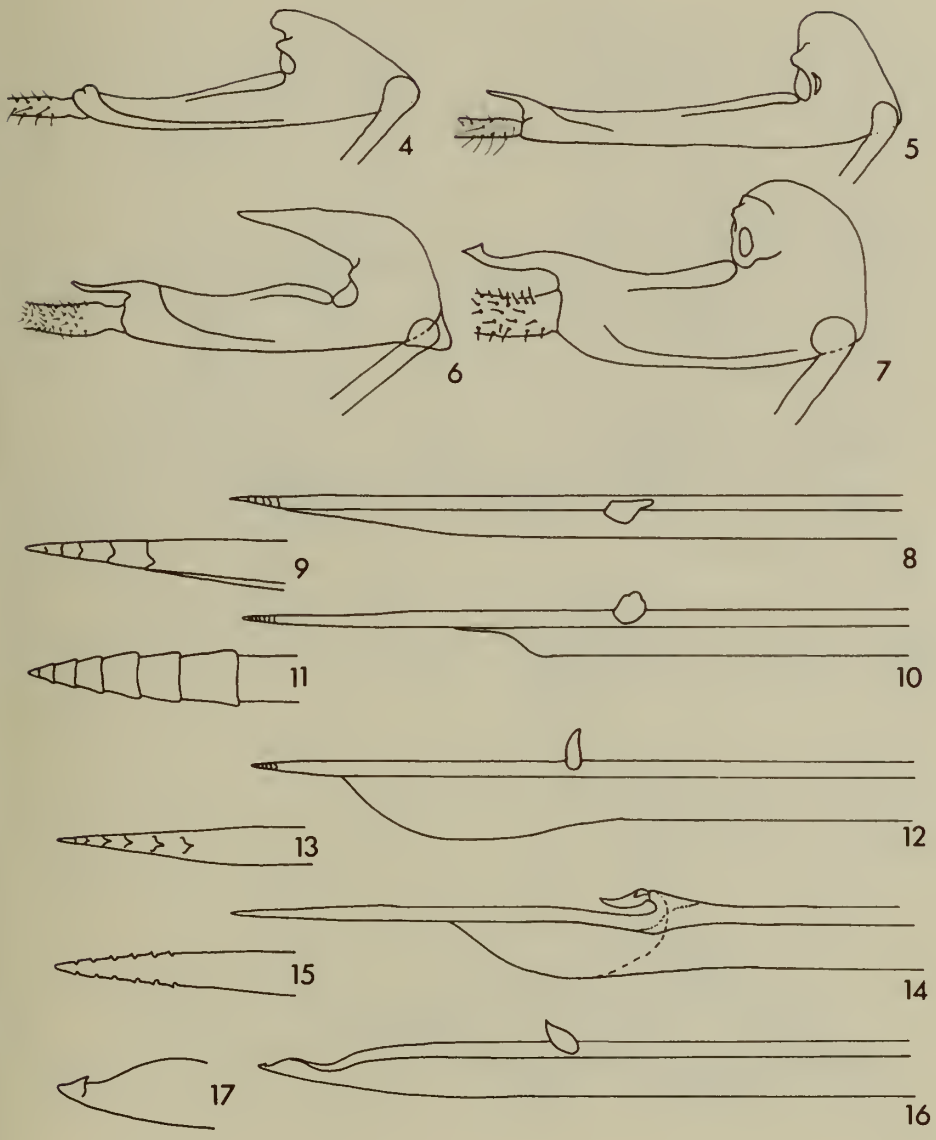
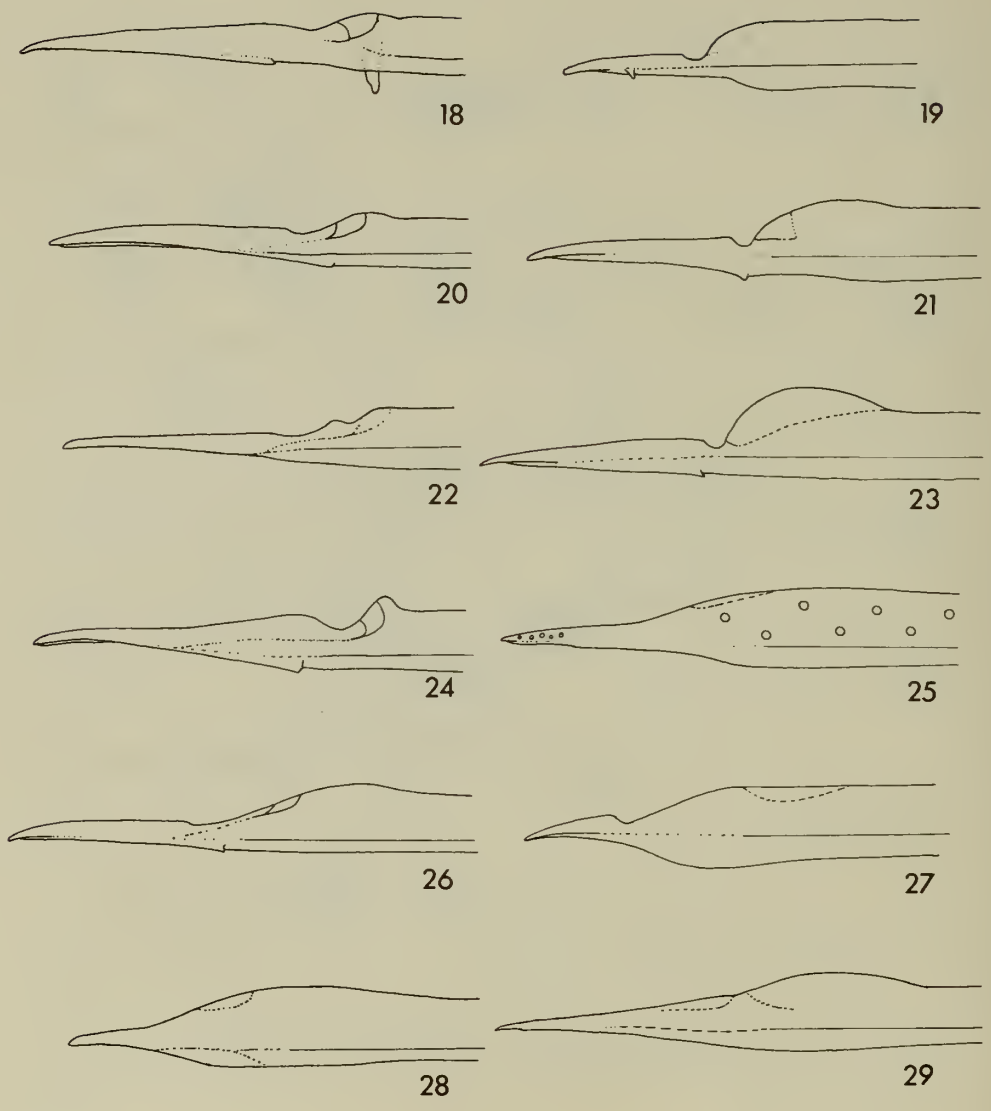


FIGS 2, 3. *Heteropelma calcator* Wesmael. 2, female terminalia; 3, valvillus.

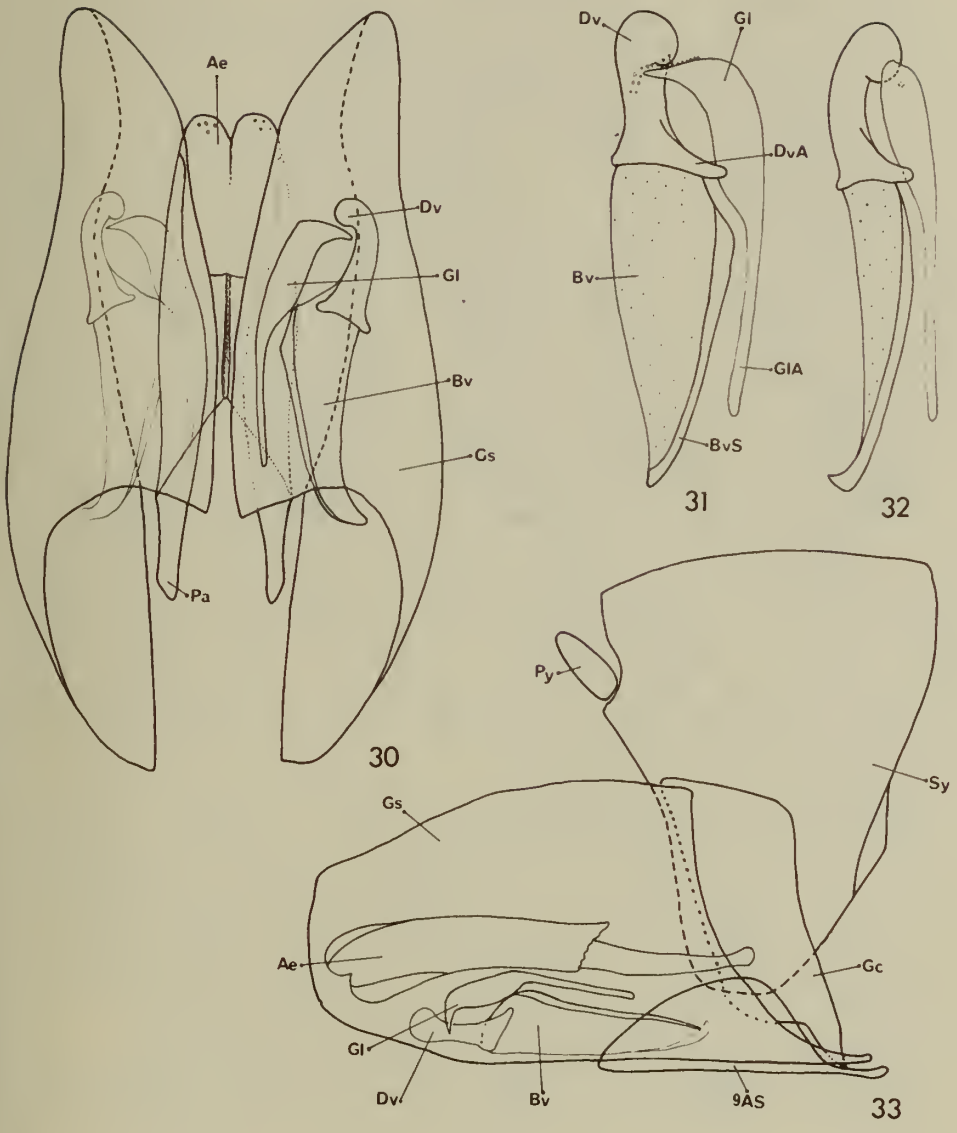


FIGS 4–7. Valvifers 2, lateral view. 4, *Anomalon foliator* (F.); 5, *Philodrymus vitticollis* (Cresson); 6, *Pseudanomalon gracile* Szépligeti; 7, *Parania tricolor* (Szépligeti).

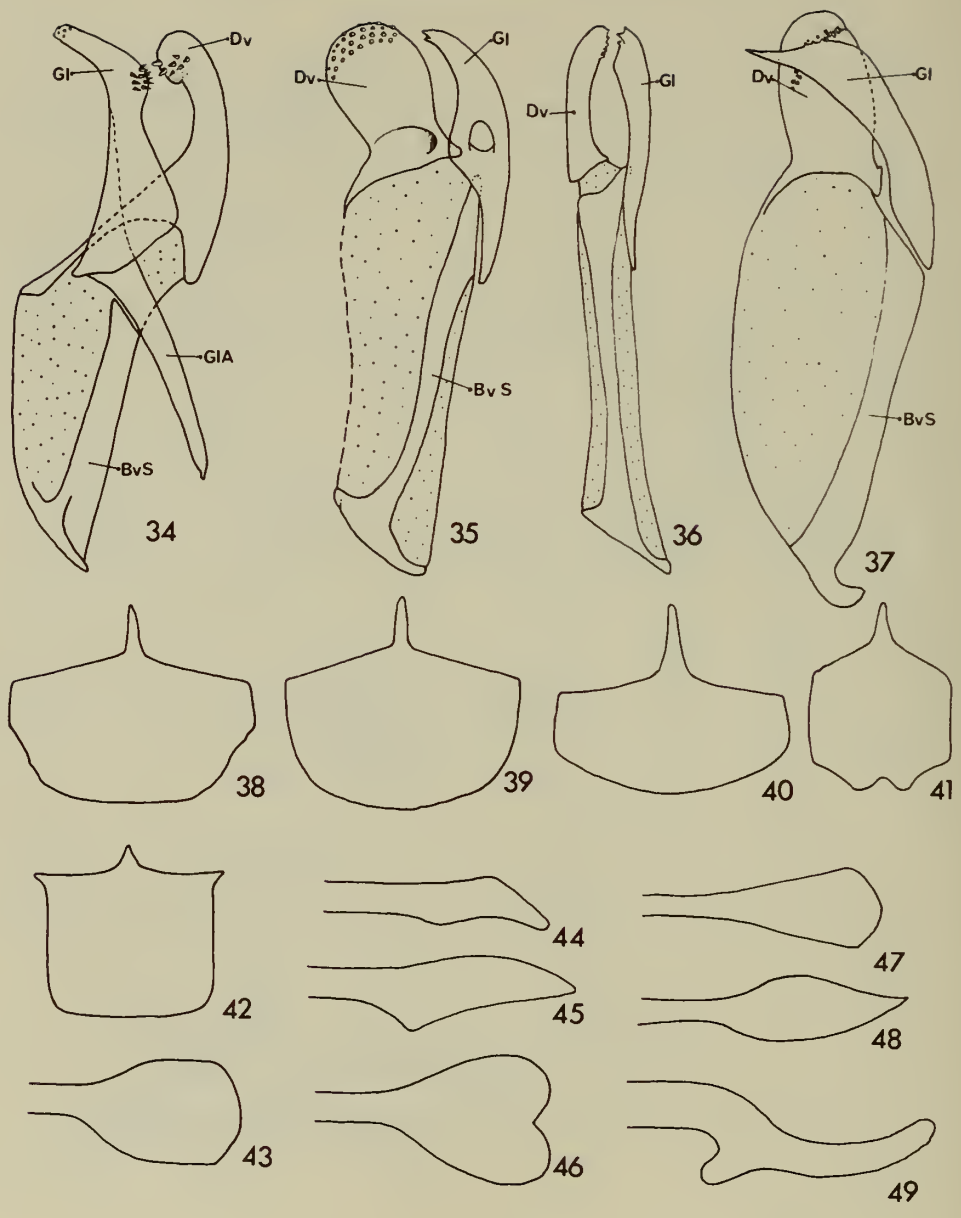
FIGS 8–17. Distal ends of valvulae 1. 8, *Anomalon foliator* (F.); 9, the same, apex enlarged; 10, *Therion circumflexum* (L.); 11, the same, apex, enlarged; 12, *Parania tricolor* (Szépligeti); 13, the same, apex enlarged; 14, *Pseudanomalon gracile* Szépligeti; 15, the same, apex enlarged; 16, *Philodrymus vitticollis* (Cresson); 17, the same, apex enlarged.



FIGS 18–29. Valvulae 2, apices, lateral view. 18, *Heteropelma amictum* (F.); 19, *Barylypa humeralis* Brauns; 20, *Trichomma fulvidens* Wesmael; 21, *Aphanistes xanthopus* (Schrank); 22, *Anomalon foliator* (F.); 23, *Gravenhorstia* (*Erigorgus*) *cerinops* (Gravenhorst); 24, *Therion circumflexum* (L.); 25, *Ophionellus fragilis* Westwood; 26, *Agrypon anxium* (Wesmael); 27, *Philodrymus vitticollis* (Cresson); 28, *Pseudanomalon gracile* Szépligeti; 29, *Parania tricolor* (Szépligeti).



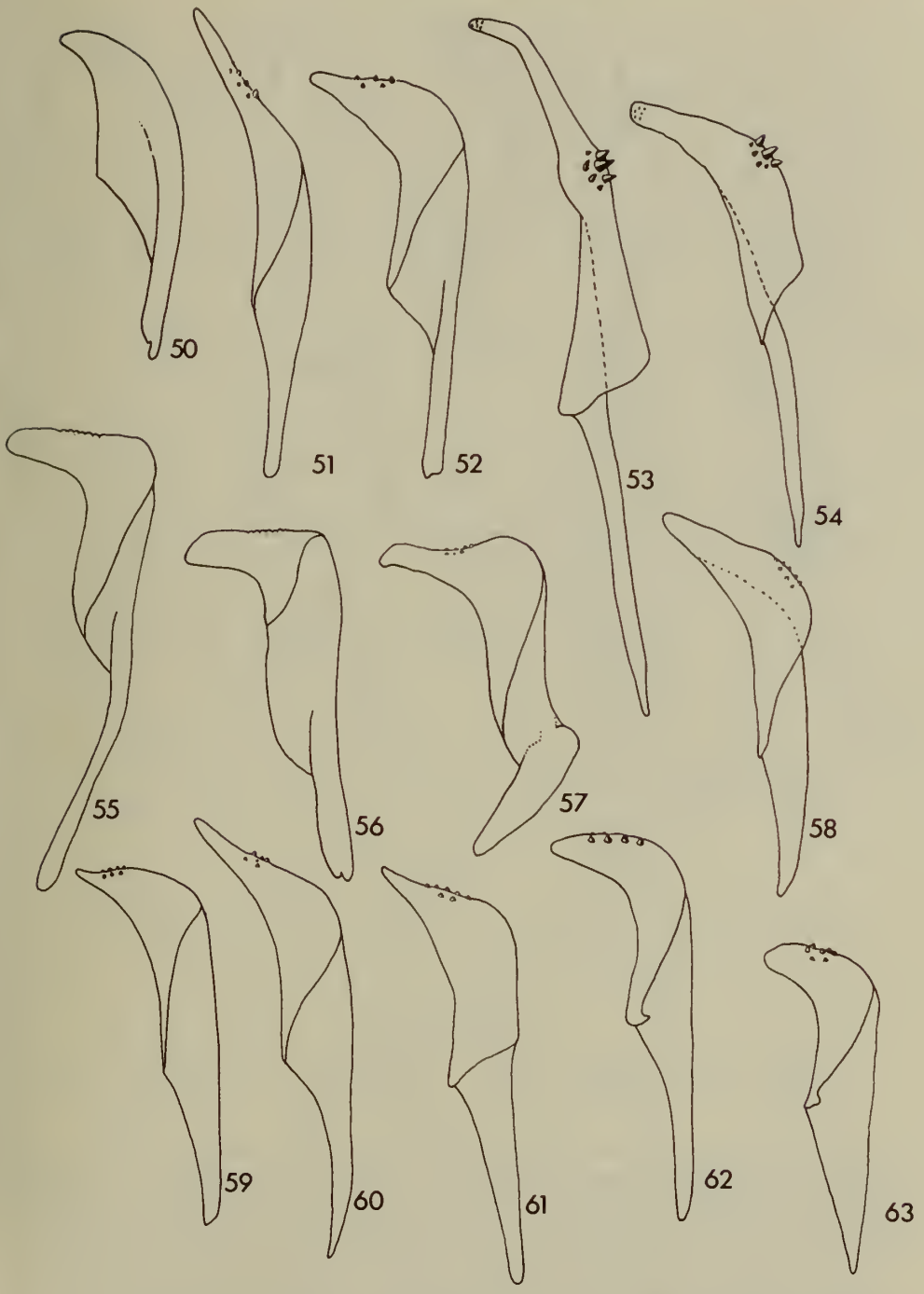
Figs 30–33. Male terminalia of *Heteropelma amictum* (F.). 30, genital capsule, ventral view; 31, clasper, lateral view; 32, the same, dorsal view; 33, genital capsule and supporting sclerites, lateral view (right half not shown). Abbreviations used in figures: Ae aedeagus; 9AS ninth abdominal sternite; Bv basivolsella; BvS basivolsellar strut; Dv distivolsella; DvA distivolsellar apodeme; Gc gonocardo; Gl gonolacinia; GlA gonolaciniar apodeme: GS gonosquama; Pa paramere; Py pygostyle; Sy syntergum.



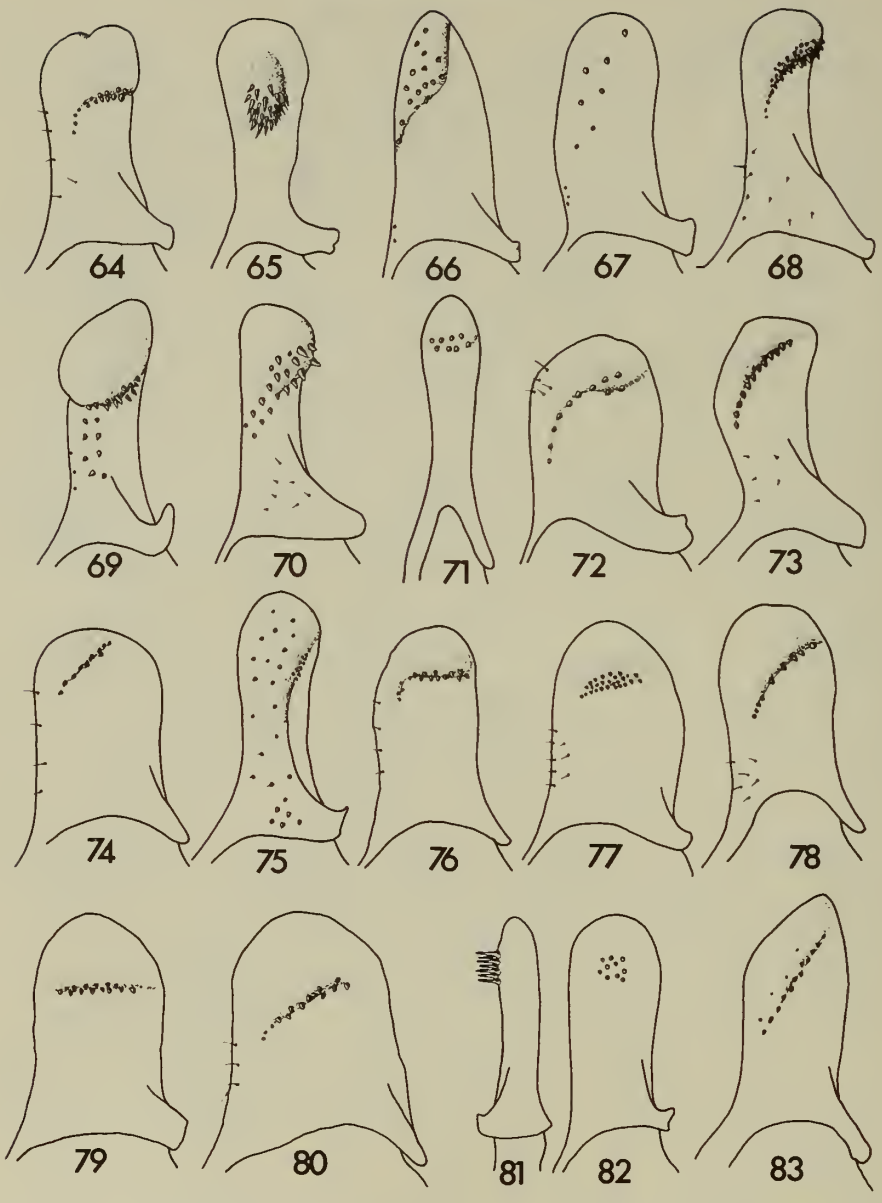
Figs 34–37. Claspers. 34, *Atrometus insignis* Foerster, lateral view; 35, *Metopius dentatus* (F.), lateral view; 36, the same, dorsal view; 37, *Ophion obscuratus* (F.), lateral view. (Labelling as for Text-fig. 30.)

Figs 38–42. Ninth abdominal sternites. 38, *Therion circumflexum* (L.); 39, *Aphanistes xanthopus* (Schrank); 40, *Pseudanomalon gracile* Szépligeti; 41, *Trichomma fulvidens* Wesmael; 42, *Ophiopterus* sp.

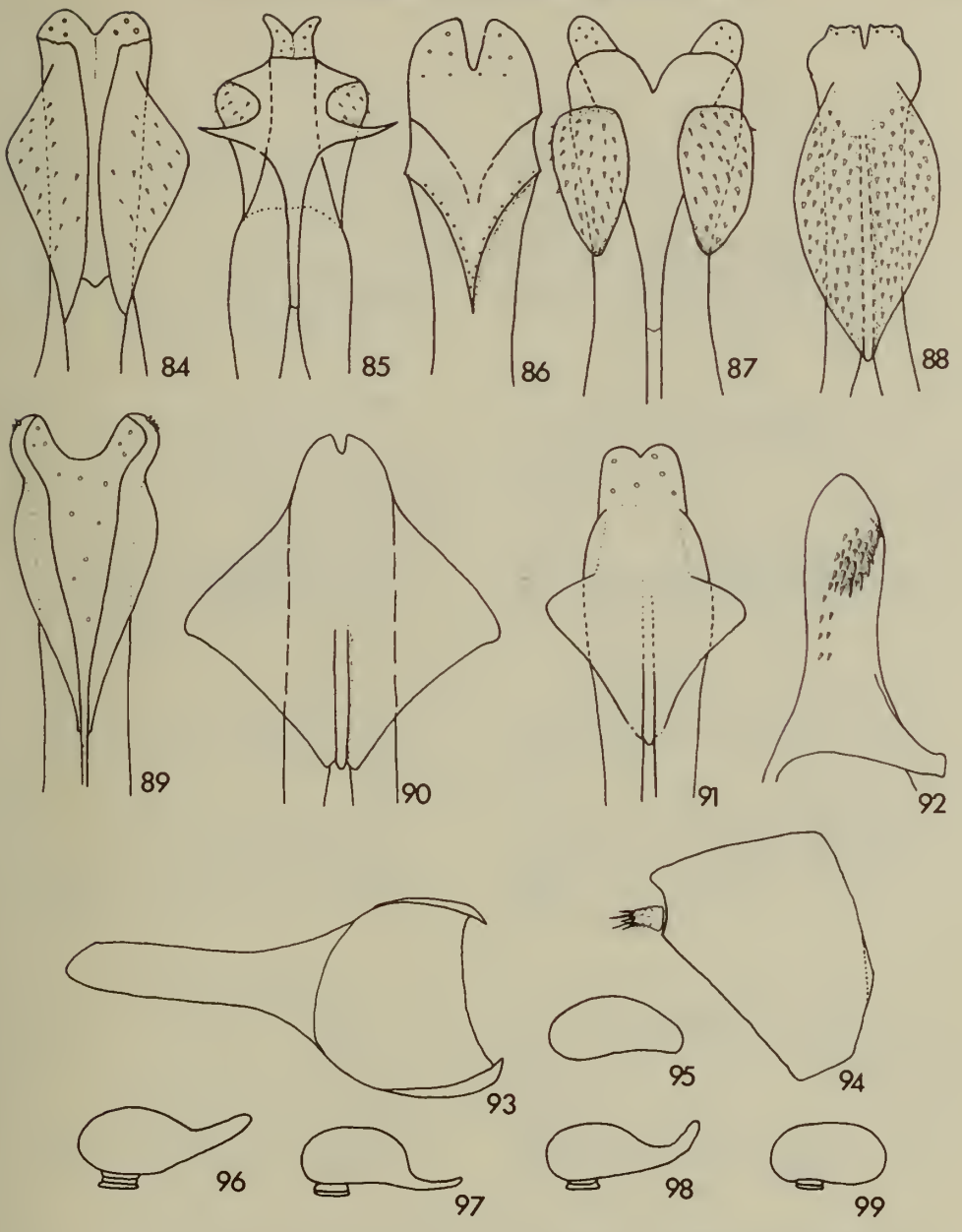
Figs 43–49. Proximal end of paramere. 43, *Clatha longipes* Cameron; 44, *Aphanistes ruficorne* (Gravenhorst); 45, *Parania tricolor* (Szépligeti); 46, *Spolas flavifrons* (Ashmead); 47, *Anomalon foliator* (F.); 48, *Vernamalon spilopterum* (Morley); 49, *Philodrymus vitticollis* (Cresson).



FIGS 50–63. Gonolaciniae (left). 50, *Anomalon foliator* (F.); 51, *Habronyx* (*Habrocampulum*) *biguttatus* (Gravenhorst); 52, *Heteropelma calcator* Wesmael; 53, *Clatha longipes* Cameron; 54, *Parania tricolor* (Szépligeti); 55, *Tanypelma datanae* (Riley); 56, *Trichomma fulvidens* Wesmael; 57, *Therion circumflexum* (L.); 58, *Spolas flavifrons* (Ashmead); 59, *Clypeocampulum tibiale* sp.n.; 60, *Habronyx* (*Camposcopus*) *nigricornis* (Wesmael); 61, *Philodrymus vitticollis* (Cresson); 62, *Vernamalon spilopterum* (Morley); 63, *Cechenodes oweni* Townes.



FIGS 64–83. Distivolsellae (left), clasping face. 64, *Barylypa carinata* (Brischke); 65, *Trichomma fulvidens* Wesmael; 66, *Vernamalon spilopterum* (Morley); 67, *Anomalon foliator* (F.); 68, *Habronyx* (*Habronyx*) *heros* (Wesmael); 69, *Therion circumflexum* (L.); 70, *Heteropelma calcator* Wesmael; 71, *Clatha longipes* Cameron; 72, *Habronyx* (*Habrocampulum*) *biguttatus* (Gravenhorst); 73, *Aphanistes xanthopus* (Schrank); 74, *Parania tricolor* (Szépligeti); 75, *Tanypelma datanae* (Riley); 76, *Perisphincter tisiphone* (Morley); 77, *Pseudanomalon gracile* Szépligeti; 78, *Podogaster* sp.; 79, *Corsoncus* sp.; 80, *Gravenhorstia* (*Erigorgus*) *cerinops* (Gravenhorst); 81, *Spolas flavifrons* (Ashmead), dorsal aspect; 82, the same, lateral aspect; 83, *Clypeocampulum tibiale* sp. n.

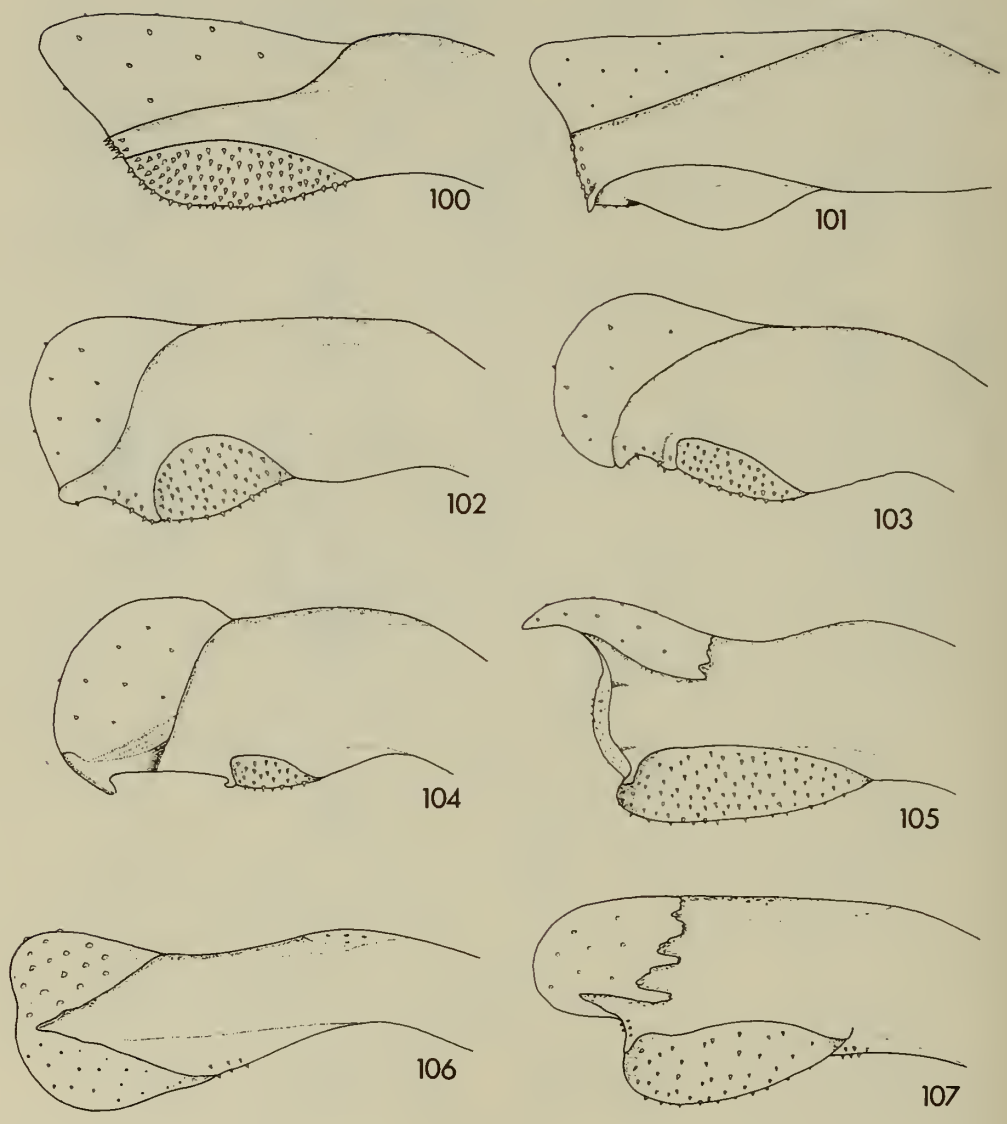


FIGS 84–91. Aedeagal apices, ventral view. 84, *Habronyx* (*Austranomalon*) *pammi* sp. n.; 85, *Corsoncus* sp.; 86, *Anomalon foliator* (F.); 87, *Habronyx* (*Habronyx*) *australasiae* (Morley); 88, *Barylypa carinata* Brischke; 89, *Philodrymus vitticollis* (Cresson); 90, *Agrypon flaveolatum* (Gravenhorst); 91, *Clypeocampulum tibiale* sp. n.

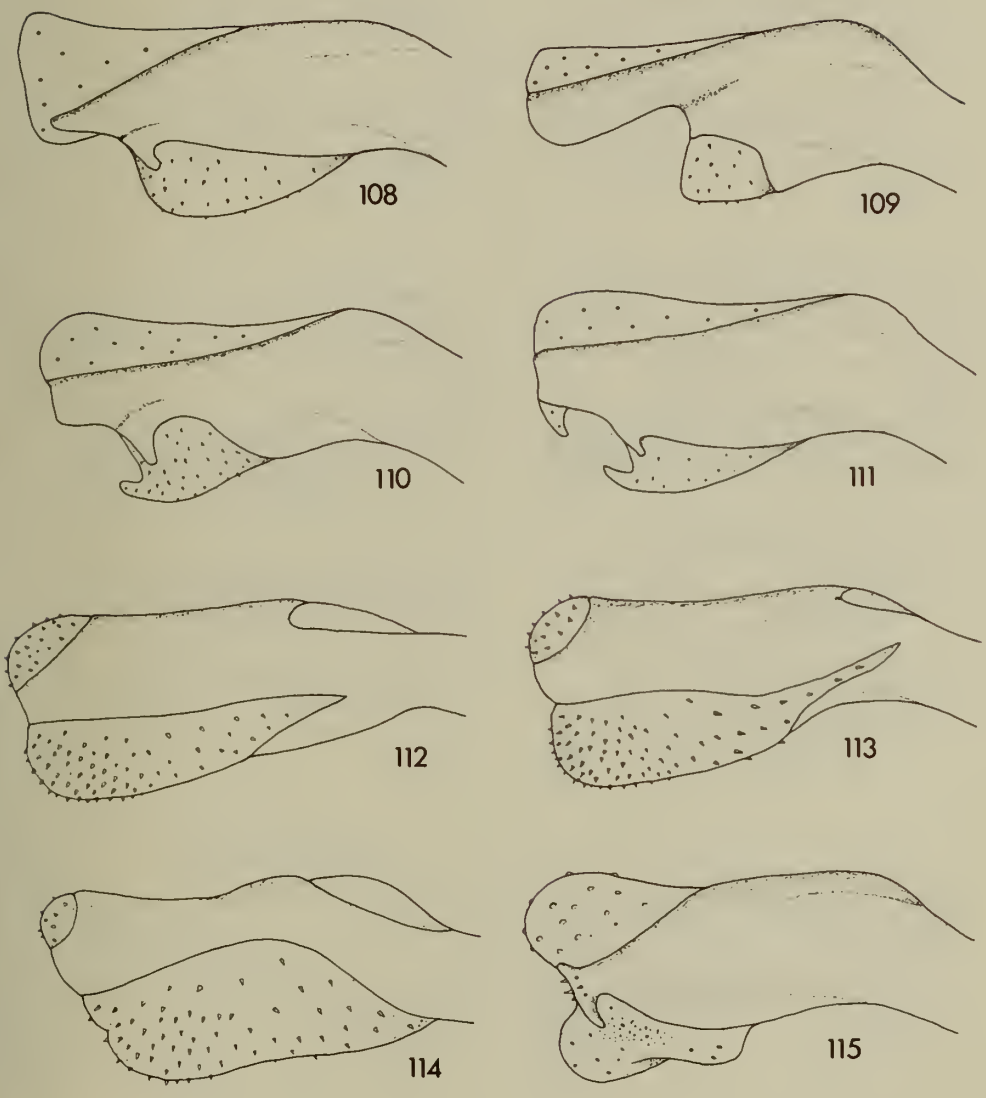
FIG. 92. Distivolsella, clasping face. *Trichomma elegantulum* Turner.

FIGS 93, 94. *Ophionellus fragilis* Westwood, ♂. 93, gonosquama, lateral view; 94, syntergum, lateral view.

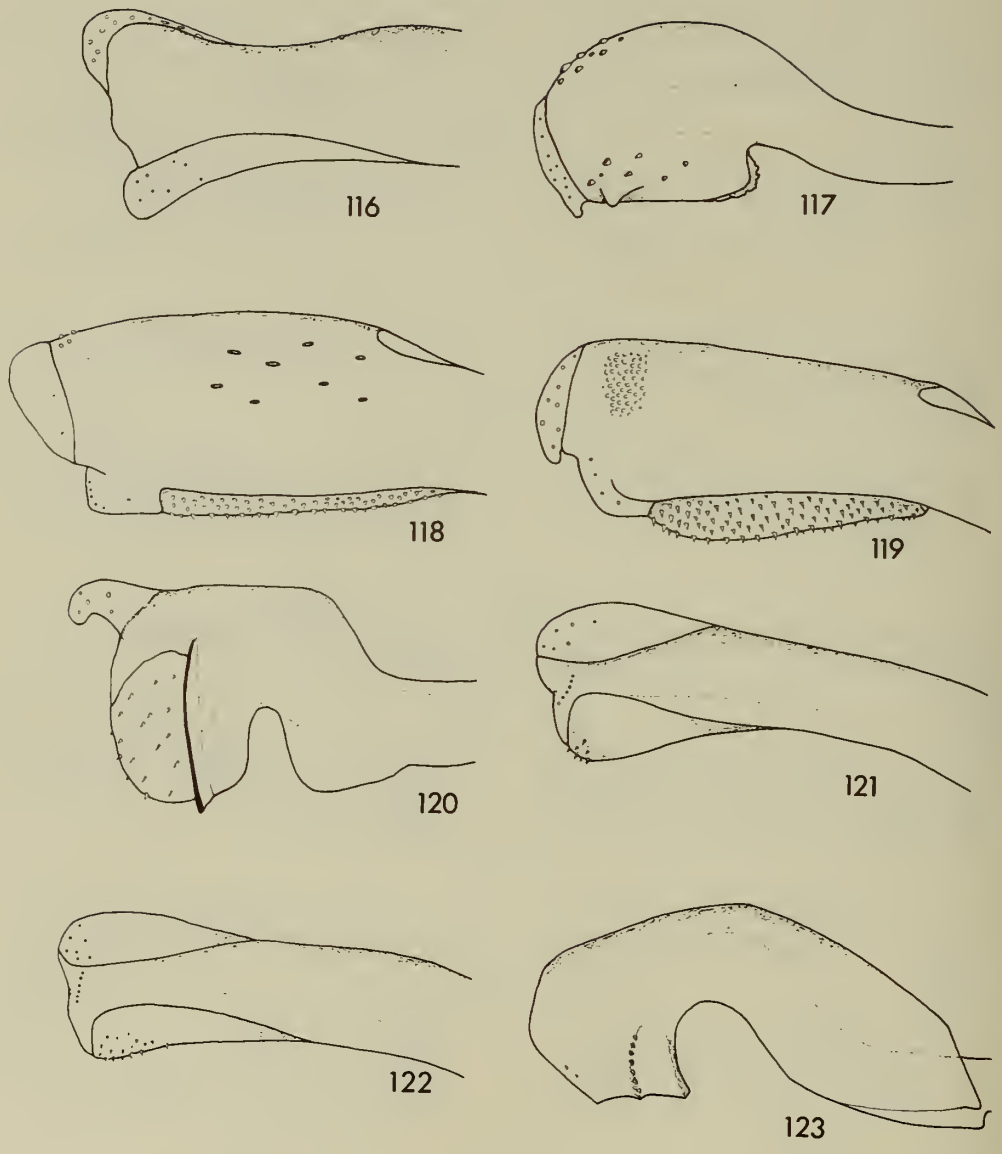
FIGS 95–99. Ovarian eggs. 95, *Gravenhorstia* (*Erigorgus*) *cerinops* (Gravenhorst); 96, *Therion circumflexum* (L.); 97, *Heteropelma calcator* Wesmael; 98, *Trichomma fulvidens* Wesmael; 99, *Aphanistes xanthopus* (Schrank).



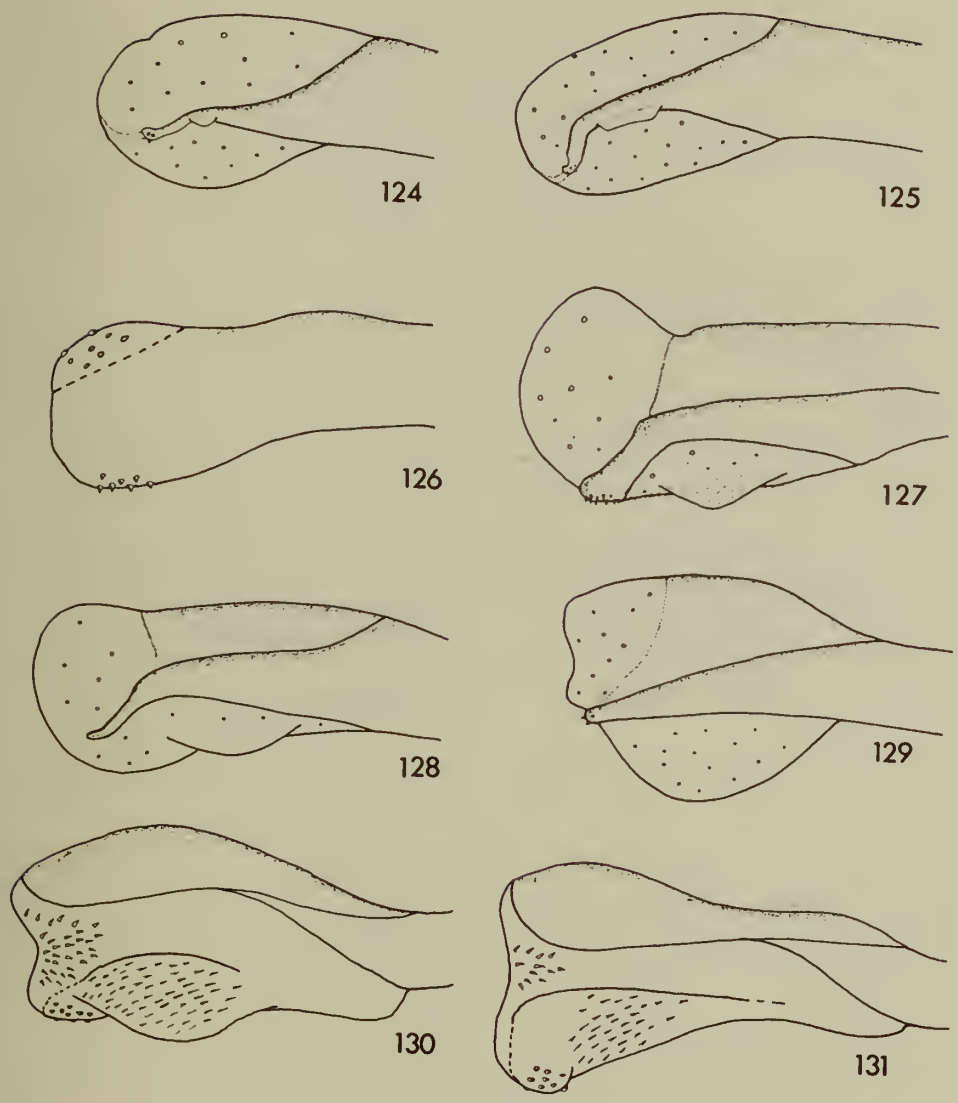
FIGS 100–107. Apices of aedeagi, lateral view. 100, *Habronyx* (*Habronyx*) *heros* (Wesmael); 101, *H.* (*Camposcopus*) *nigricornis* (Wesmael); 102, *H.* (*Habronyx*) *orbitale* (Morley); 103, *H.* (*H.*) *insidiator* (Smith); 104, *H.* (*H.*) *pyretorus* (Cameron); 105, *H.* (*H.*) *australasiae* (Morley); 106, *H.* (*Habrocampulum*) *biguttatus* (Gravenhorst); 107, *H.* (*Austranomalon*) *pammi* sp. n.



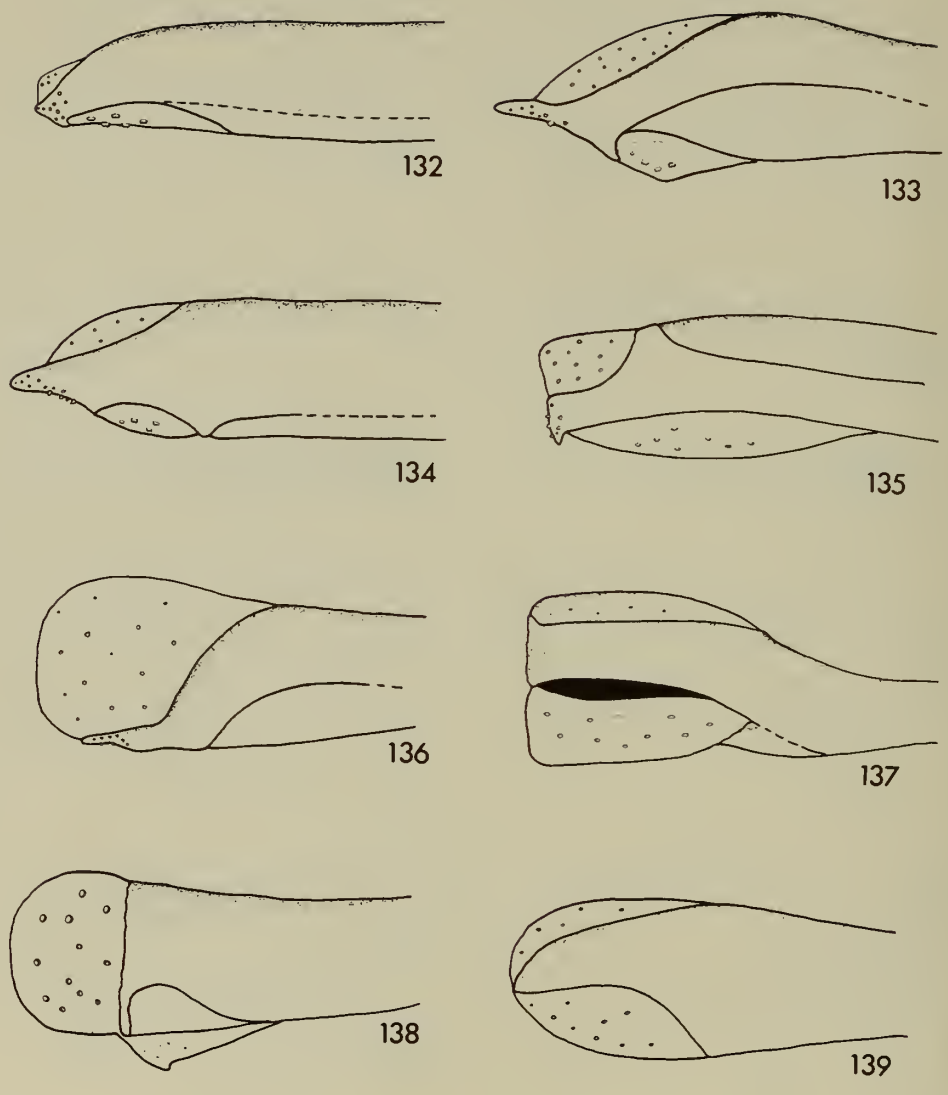
FIGS 108–115. Apices of aedeagi, lateral view. 108, *Gravenhorstia* (*Erigorgus*) *cerinops* (Gravenhorst); 109, *G.* (*E.*) *nigrita* (Norton); 110, *G.* (*Kokujewiella*) *ibera* (Ceballos); 111, *G.* (*Gravenhorstia*) *picta* Boie; 112, *Aphanistes xanthopus* (Schrank); 113, *A. ruficornis* (Gravenhorst); 114, *A. variicolor* (Morley); 115, *Clypeocampulum tibiale* sp. n.



Figs 116–123. Apices of aedeagi, lateral view. 116, *Encardia picta* Tosquinet; 117, *Pseudanomalon gracile* Szépligeti; 118, *Barylypa carinata* Brischke; 119, *B. delictor* (Thunberg); 120, *Corsoncus* sp.; 121, *Tanypelma datanae* (Riley); 122, *Heteropelma calcator* Wesmael; 123, *Therion circumflexum* (L.).



FIGS 124–131. Apices of aedeagi, lateral view. 124, *Podogaster coarctata* Brullé; 125, *Philodrymus vitticollis* (Cresson); 126, *Ophionellus fragilis* Westwood; 127, *Perisphincter* sp.; 128, *Phaenolabrorychus anisiti* Viereck; 129, *Agrypon flaveolatum* (Gravenhorst); 130, *Trichomma fulvidens* Wesmael; 131, *T. elegantulum* Turner.



FIGS 132–139. Apices of aedeagi, lateral view. 132, *Parania tricolor* (Szépligeti); 133, *Spolas flavifrons* (Ashmead); 134, *Clatha longipes* Cameron; 135, *Atrometus insignis* Foerster; 136, *Vernamalon spilopterum* (Morley); 137, *Cechenodes oweni* Townes; 138, *Ophiopterus* sp.; 139, *Metoa exilis* (Provancher).

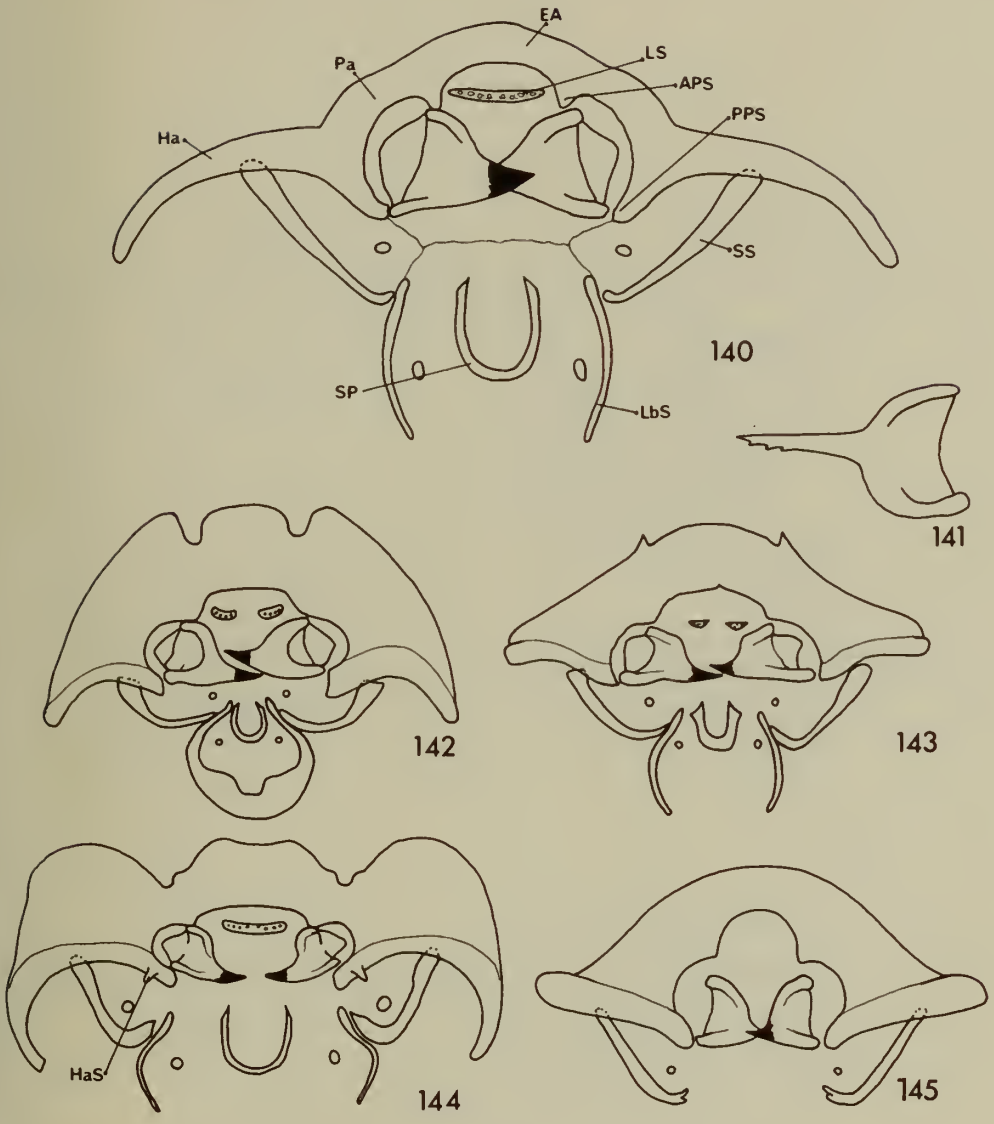
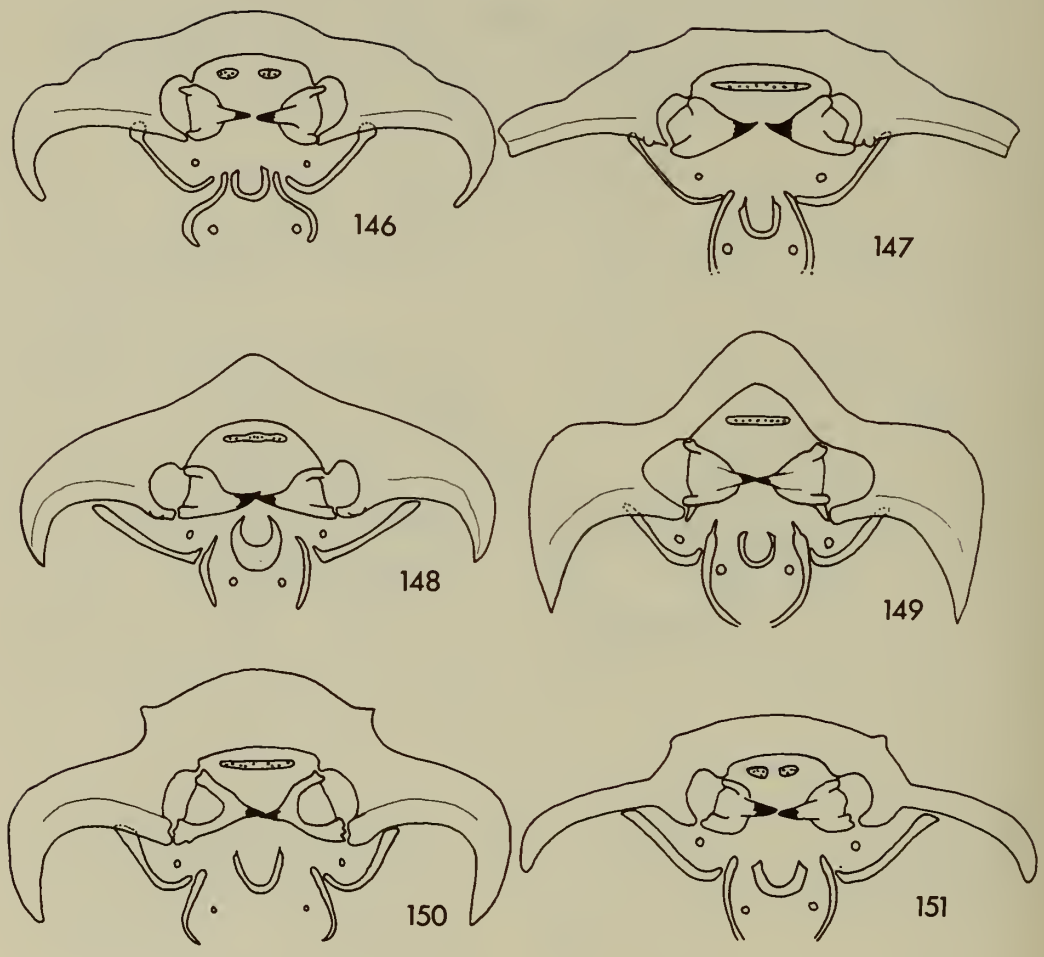


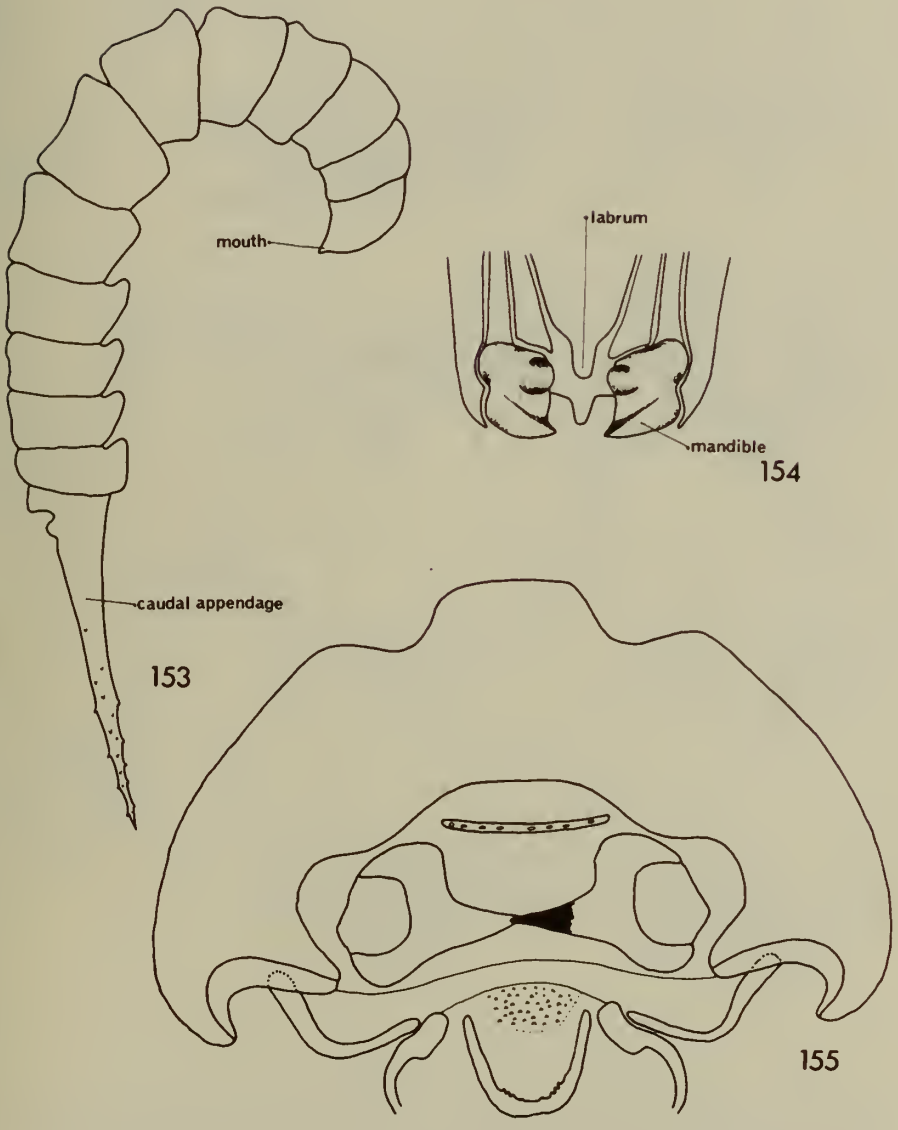
FIG. 140. Cephalic capsule of final instar larva of *Habronyx* (*Camposcopus*) *nigricornis* Wesmael.

FIG. 141. Mandible of final instar larva of *Anomalon* sp.

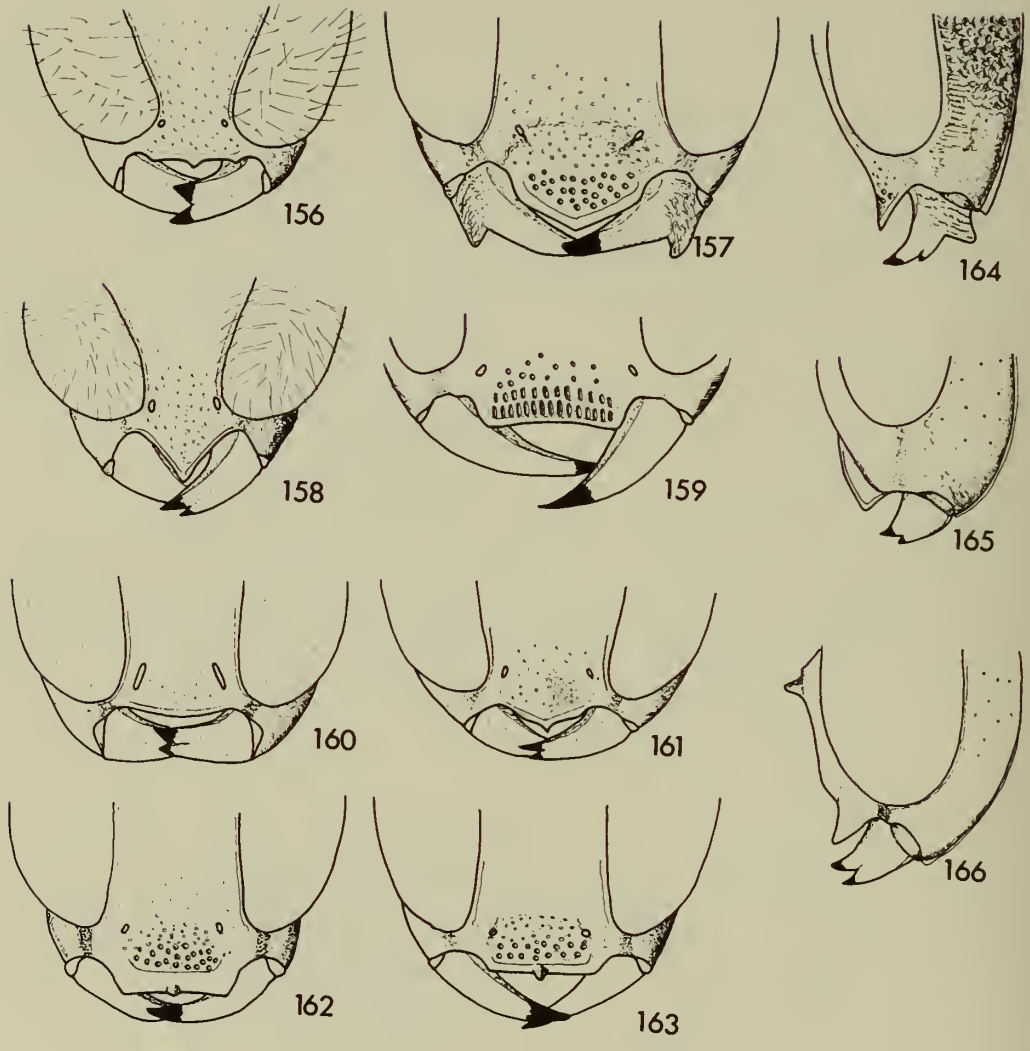
FIGS 142–145. Cephalic capsules of final instar larvae. 142, *Heteropelma capitatum* (Desvignes); 143, *Therion brevicorne* (Gravenhorst); 144, *Habronyx* (*Habronyx*) *pyretorus*? (Cameron); 145, *Trichomma enecator* (Rossi). Abbreviations used in figures: APS anterior pleurostomal process; EA epistomal arch; Ha hypostoma; HaS hypostomal spur; LbS labial sclerite; LS labral sensillae; Pa pleurostoma; PPS posterior pleurostomal process; SP silk press; SS stipital sclerite.



FIGS 146–151. Cephalic capsules of final instar larvae. 146, *Perisphincter* sp.; 147, *Gravenhorstia* (*Erigorgus*) *melanops* (Foerster); 148, *Habronyx* (*Austranomalon*) *pammi* sp. n.; 149, *Parania tricolor* (Szépligeti); 150, *Aphanistes bellicosus* (Wesmael); 151, *Agrypon anxium* (Wesmael).

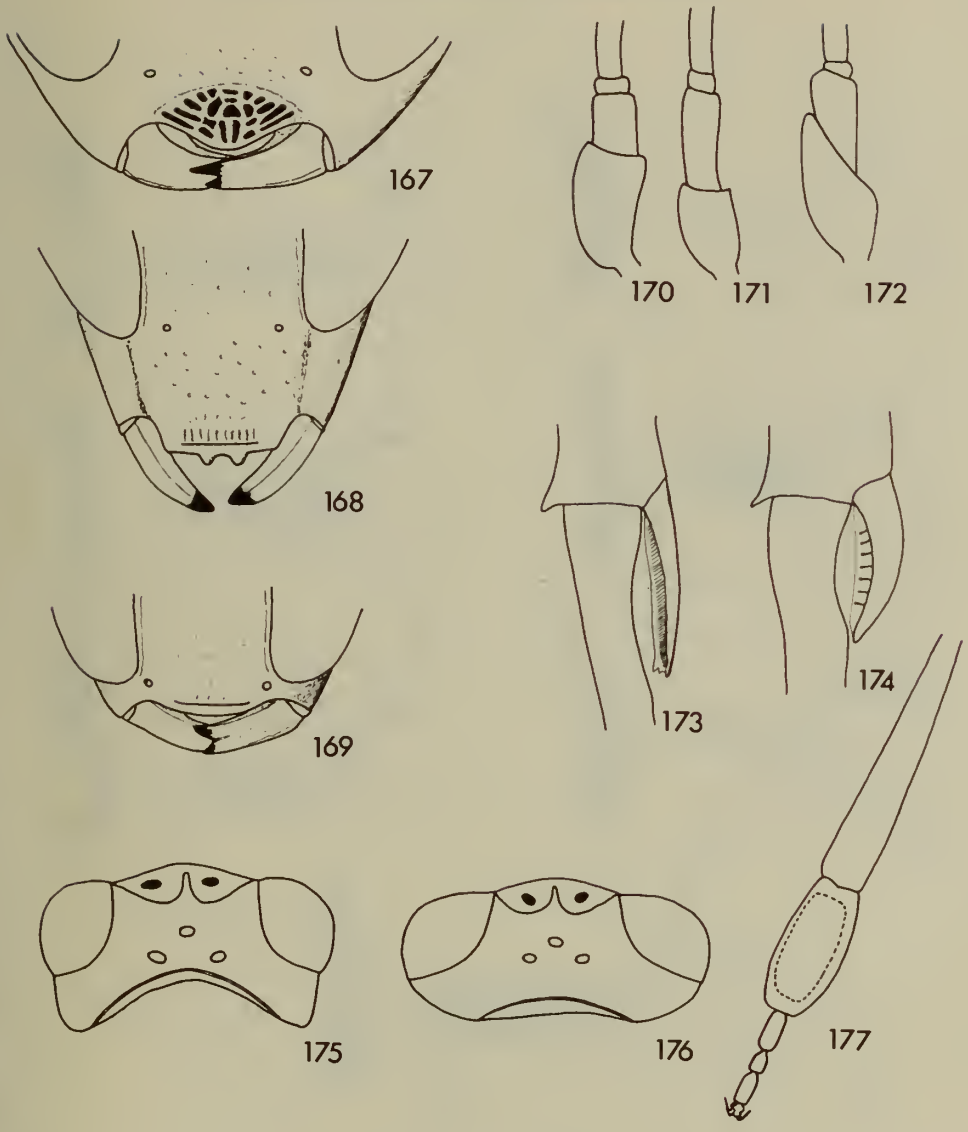


FIGS 153–155. *Encardia picta* Tosquinet. 153, first instar larva, entire; 154, first instar larva, mouth, dorsal view; 155, cephalic capsule of final instar larva.



Figs 156–163. Lower faces, anterior view. 156, *Trichomma* sp. (South American); 157, *Gravenhorstia* (*Ribasia*) *erythrogaster* (Ceballos); 158, *Trichomma enecator* (Rossi); 159, *Aubertiana unidentator* (Aubert); 160, *Habronyx* (*Austranomalon*) *pammi* sp. n.; 161, *Gravenhorstia* (*Erigorgus*) *latro* (Schrank); 162, *G.* (*E.*) *nigrita* (Norton); 163, *G.* (*E.*) *buccata* (Morley).

Figs 164–166. Heads, lateral view. 164, *Gravenhorstia* (*Ribasia*) *erythrogaster* (Ceballos); 165, *Habronyx* (*Habronyx*) *australasiae* (Morley); 166, *Gravenhorstia* (*Gravenhorstia*) *picta* Boie.



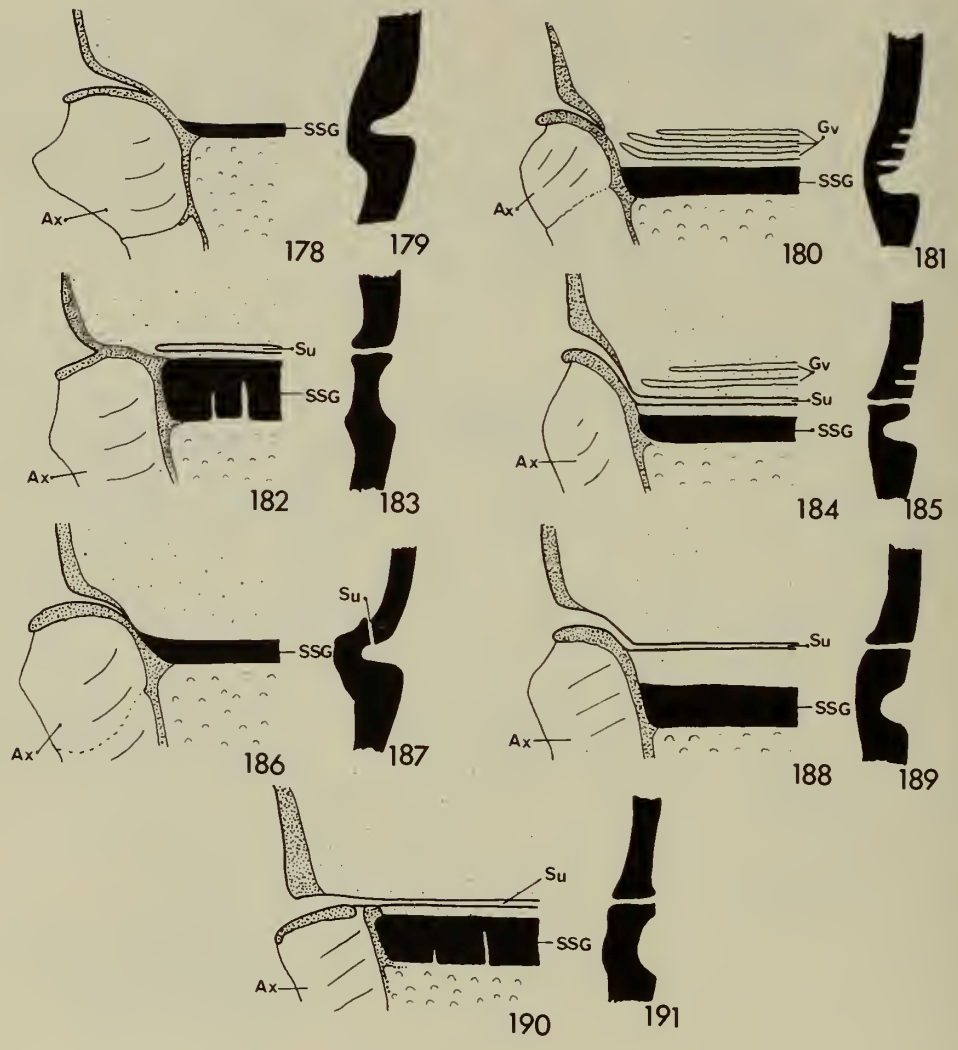
Figs 167–169. Lower faces, anterior view. 167, *Clypeocampulum tibiale* sp. n.; 168, *Anomalon rufipes* (Cameron); 169, *A. foliator* (F.).

Figs 170–172. Basal antennal segments. 170, *Trichomma fulvidens* Wesmael; 171, *Phaenolabrorychus anisitsi* Viereck; 172, *Ophiopterus* sp.

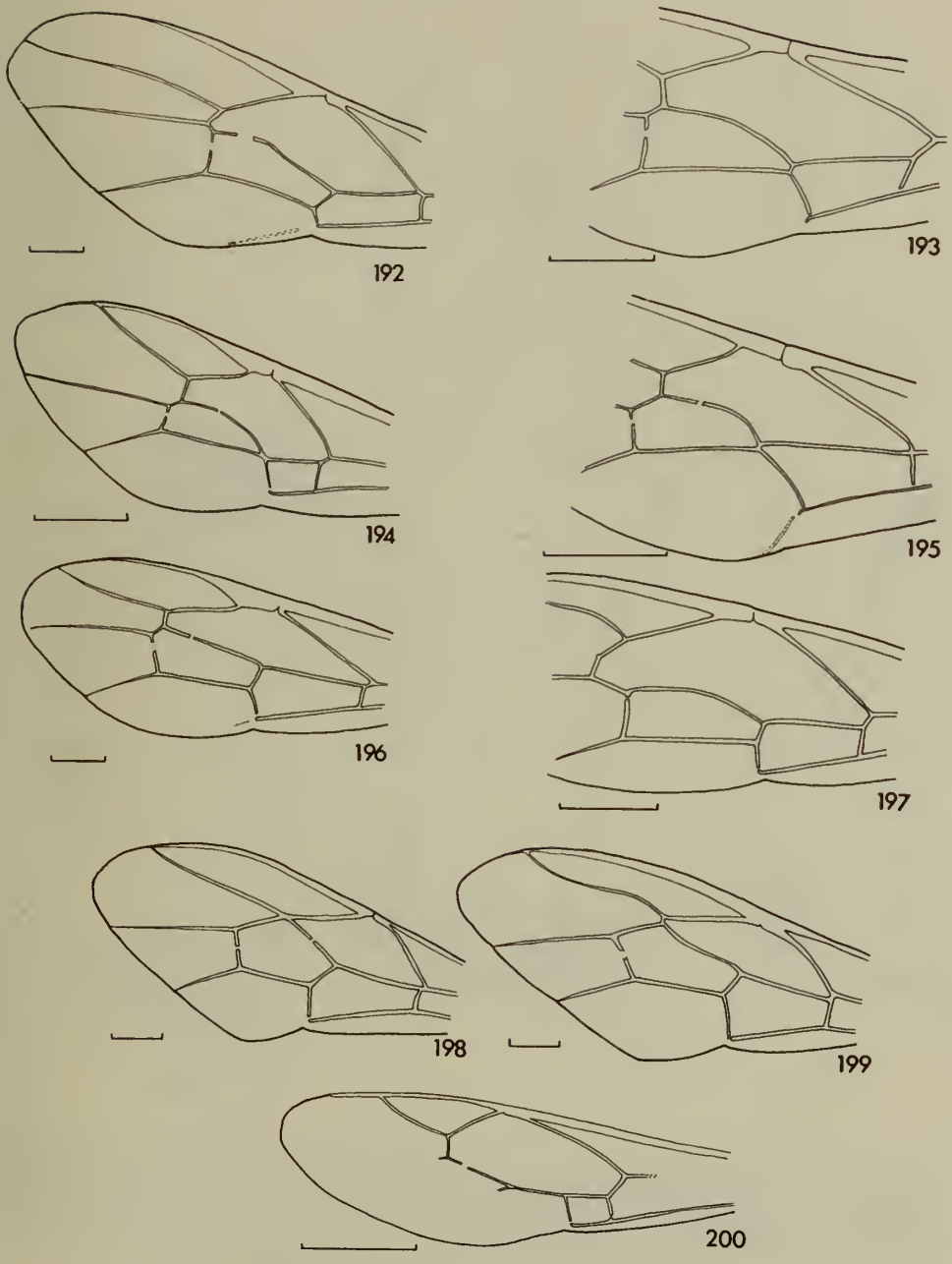
Figs 173, 174. Fore tibial spurs. 173, *Heteropelma capitatum* (Desvignes); 174, *Trichomma fulvidens* Wesmael.

Figs 175, 176. Heads, dorsal view. 175, *Heteropelma scaposum* (Morley); 176, *H. perornatum* (Cameron).

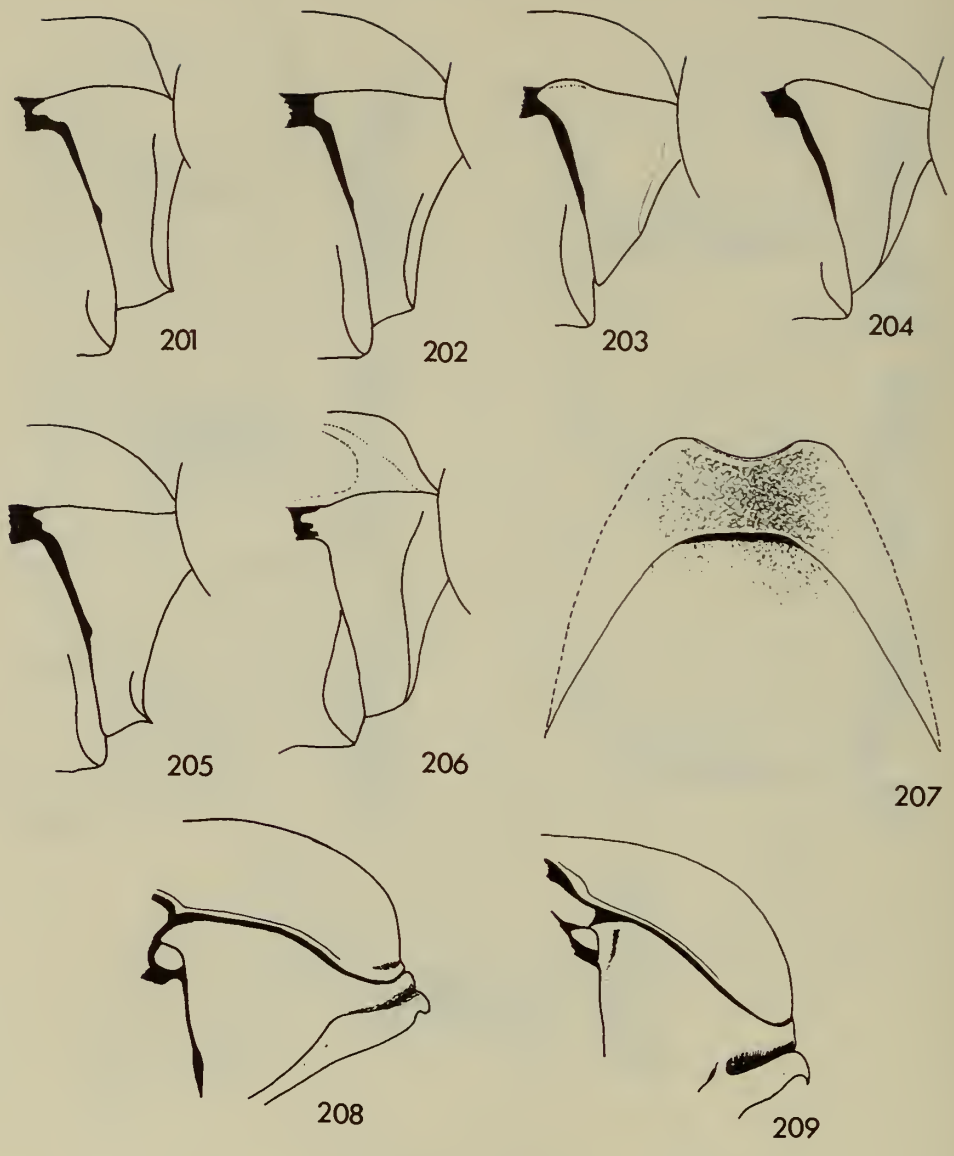
Fig. 177. Hind tarsi, ventral view. *Heteropelma capitatum* (Desvignes).



Figs 178–191. Scuto-scutellar regions. 178, *Agrypon anxium* (Wesmael); 179, the same, median longitudinal section; 180, *Phaenolabrorychus anisitsi* Viereck; 181, the same, median longitudinal section; 182, *Agrypon albiditarsus* Morley; 183, the same, median longitudinal section; 184, *Ophiopterus coarctatus* Brullé; 185, the same, median longitudinal section; 186, *Vernamalon spilopterum* (Morley); 187, the same, median longitudinal section; 188, *Ophionellus fragilis* Westwood; 189, the same, median longitudinal section; 190, *Philodrymus vitticollis* (Cresson); 191, the same, median longitudinal section. Abbreviations used in figures: Ax axilla; Gv groove; SSG scuto-scutellar groove; Su suture. Coarse stippling denotes carinae, fine stippling the mesoscutum and inverted-U shading the scutellum.



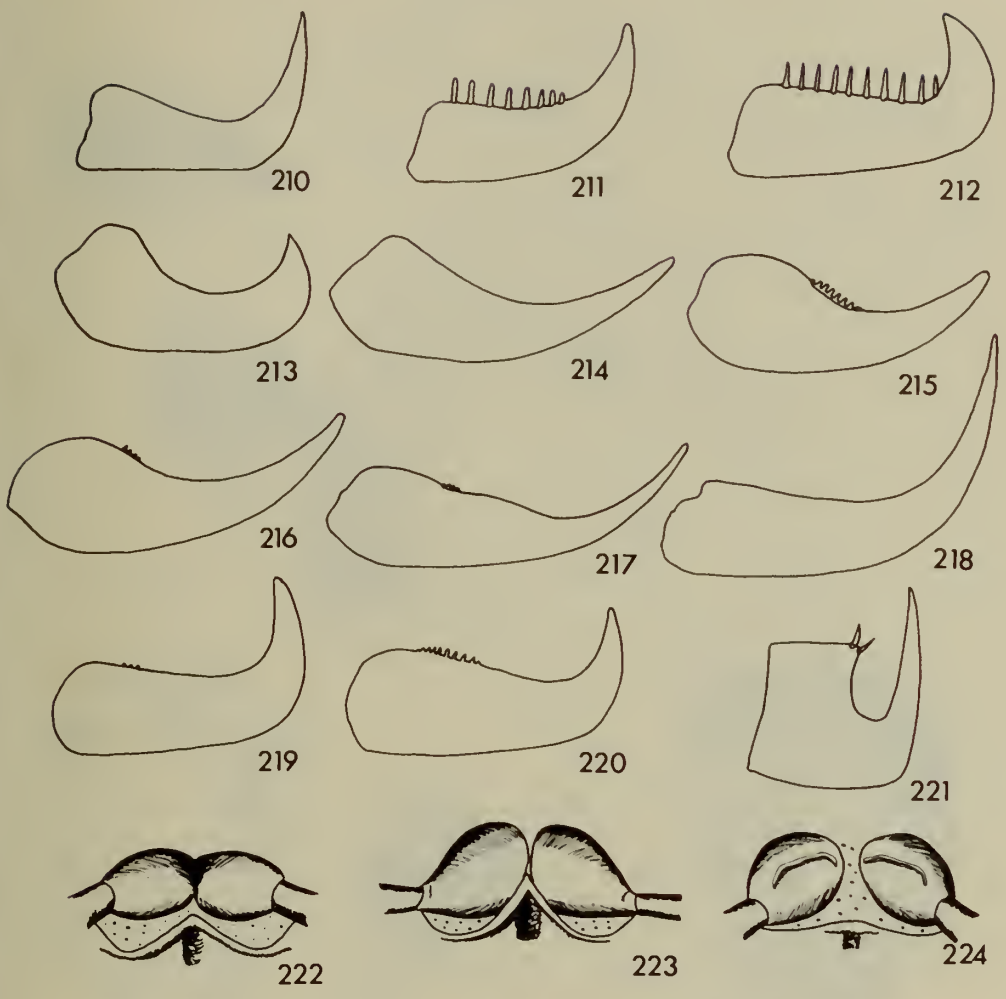
FIGS 192–200. Left forewings. 192, *Pseudanomalon gracile* Szépligeti; 193, *Phaenolabrorychus anisitsi* Viereck; 194, *Parania tricolor* (Szépligeti); 195, *Podogaster* sp.; 196, *Heteropelma scaposum* (Morley); 197, *Ophiopterus* sp.; 198, *Brachynervus tsunekii* Uchida; 199, *B. confusus* sp. n.; 200, *Ophionellus* sp. (Scale line = 1 mm.).



FIGS 201–206. Pronotum and anterior of mesoscutum in profile. 201, *Habronyx* (*Habrocampulum*) *biguttatus* (Gravenhorst); 202, *Therion circumflexum* (L.); 203, *Spolas flavifrons* (Ashmead); 204, *Gravenhorstia* (*Erigorgus*) *latro* (Schrank); 205, *Heteropelma scaposum* (Morley); 206, *Habronyx* (*Camposcopus*) *nigricornis* (Wesmael).

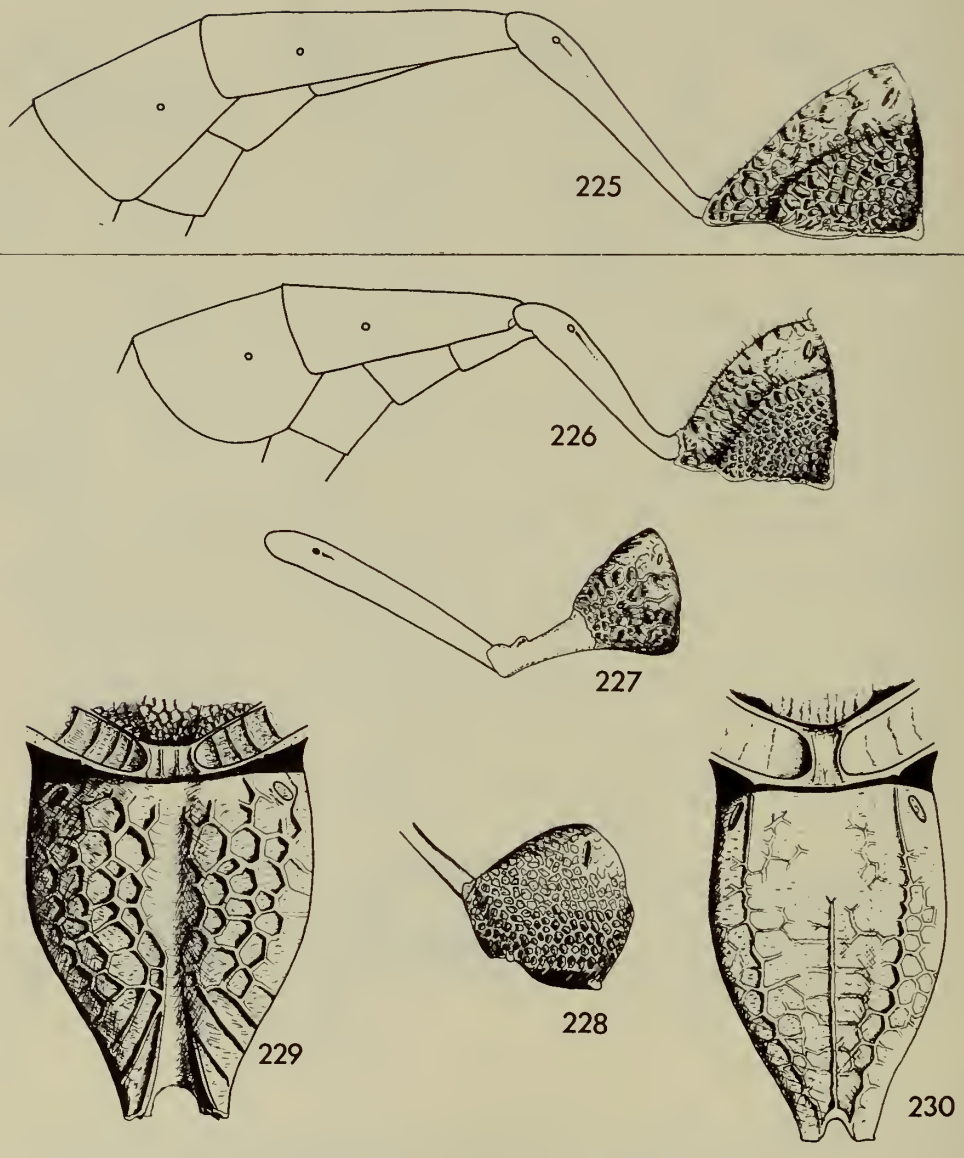
FIG. 207. Pronotum and anterior of mesoscutum, dorsal view. *Barylypa humeralis* Brauns.

FIGS 208, 209. Pronotum and anterior of mesoscutum, dorso-anterio-lateral aspect. 208, *Aphanistes ruficornis* (Gravenhorst); 209, *Gravenhorstia* (*Gravenhorstia*) *picta* Boie. (Figs 208–209 drawn from electronmicrographs.)



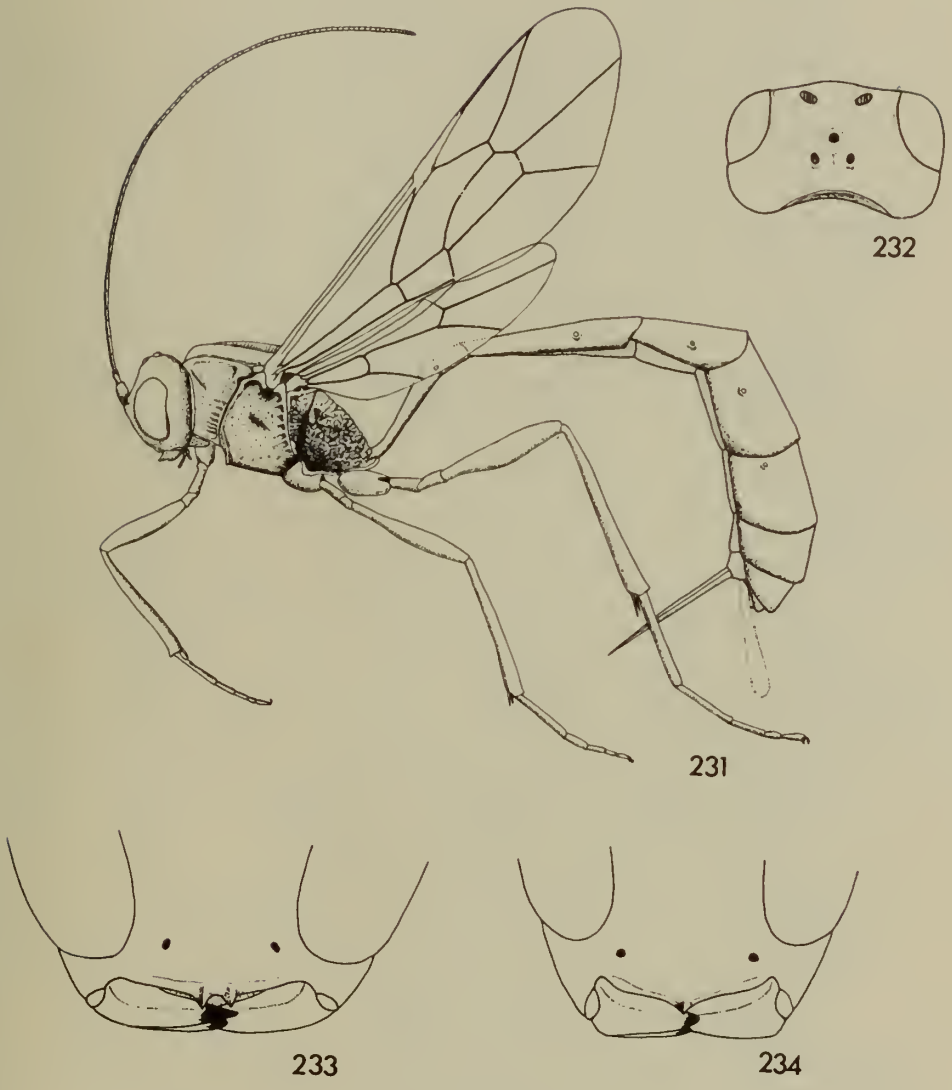
FIGS 210–221. Hind tarsal claws. 210, *Habronyx* (*Habronyx*) *insidiator* (Smith) ♂; 211, *H.* (*H.*) *heros* (Wesmael) ♂; 212, *Aphanistes bellicosus* (Wesmael) ♂; 213, *Habronyx* (*Austranomalon*) *pammi* sp. n. ♀; 214, the same, ♂; 215, *Gravenhorstia* (*Erigorgus*) *latro* (Schrank), ♀; 216, the same, ♂; 217, *G.* (*E.*) *melanobatus* (Gravenhorst) ♀; 218, the same, ♂; 219, *Habronyx* (*Habrocampulum*) *biguttatus* (Gravenhorst) ♀; 220, the same, ♂; 221, *Heteropelma calcator* Wesmael ♀.

FIGS 222–224. Fore coxae, ventral view. 222, *Atrometus insignis* Foerster; 223, *Podogaster coarctata* Brullé; 224, *Agrypon anxium* (Wesmael).



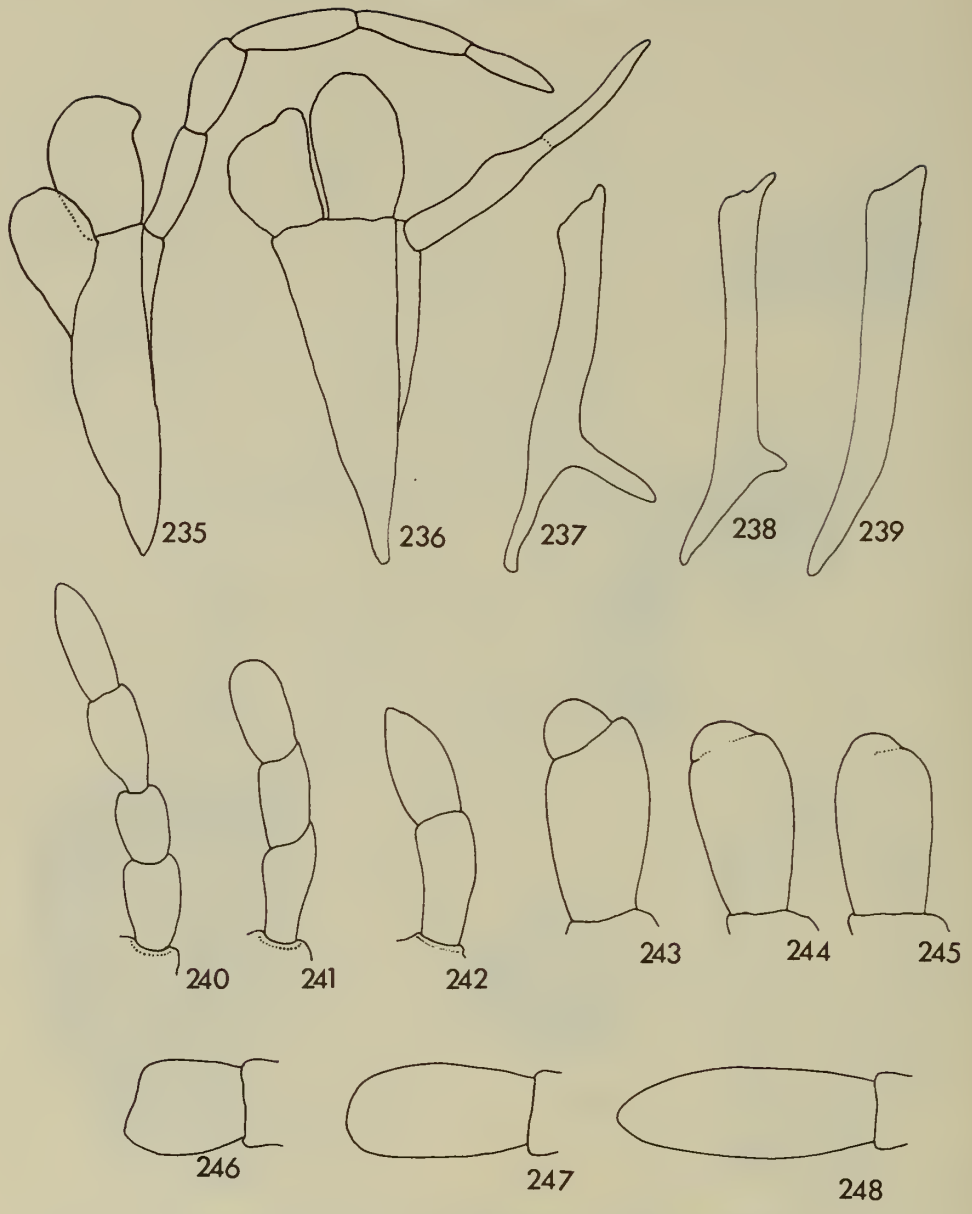
Figs 225–228. Propodeum and basal segments of gaster, lateral view. 225, *Gravenhorstia* (*Erigorgus*) *cerinops* (Gravenhorst); 226, *G.* (*Kokujewiella*) *ibera* (Ceballos); 227, *Cechenodes oweni* Townes; 228, *Brachynervus confusus* sp. n.

Figs 229, 230. Propodeum, dorsal view. 229, *Habronyx* (*Habronyx*) *heros* (Wesmael); 230, *H.* (*Habrocampulum*) *biguttatus* (Gravenhorst).



FIGS 231–233. *Vernamalon spilopterum* (Morley). 231, ♀ entire; 232, head, dorsal view; 233, lower face, anterior view.

FIG. 234. *Bimentum* sp., lower face, anterior view.



Figs 235, 236. Right maxillae. 235, *Barylypa carinata* Brischke; 236, *Encardia picta* Tosquinet.

Figs 237–239. Right cardina. 237, *Agrypon flaveolatum* (Gravenhorst); 238, *Gravenhorstia* (*Erigorgus*) *cerinops* (Gravenhorst); 239, *Anomalon foliator* (F.).

Figs 240–242. Labial palps. 240, *Gravenhorstia* (*Erigorgus*) *cerinops* (Gravenhorst); 241, *Trichomma enecator* (Rossi); 242, *Encardia picta* Tosquinet.

Figs 243–245. Distal segments of labial palps of *Agrypon anxium* Wesmael. 243, segments 3 and 4 separate; 244, segment 4 partially fused to segment 3; 245, segment 4 virtually entirely fused to segment 3.

Figs 246–248. Variation in shape of terminal segments of labial palps of *Therion circumflexum* (L.). (Figs 235–248 drawn from slides prepared from females only.)

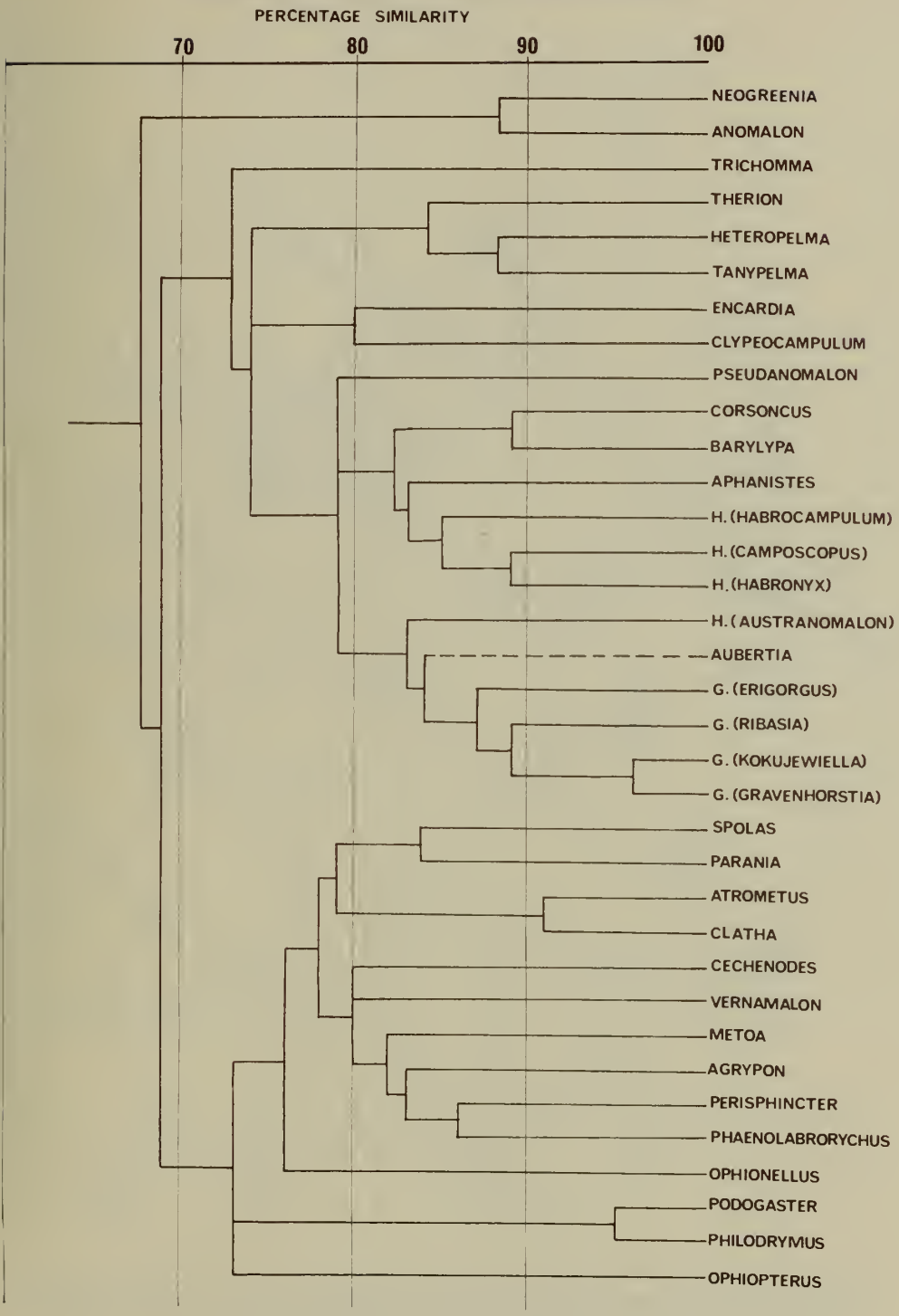


FIG. 249. Dendrogram showing the phenetic interrelationships between genera as represented by the type-species of the several genera.

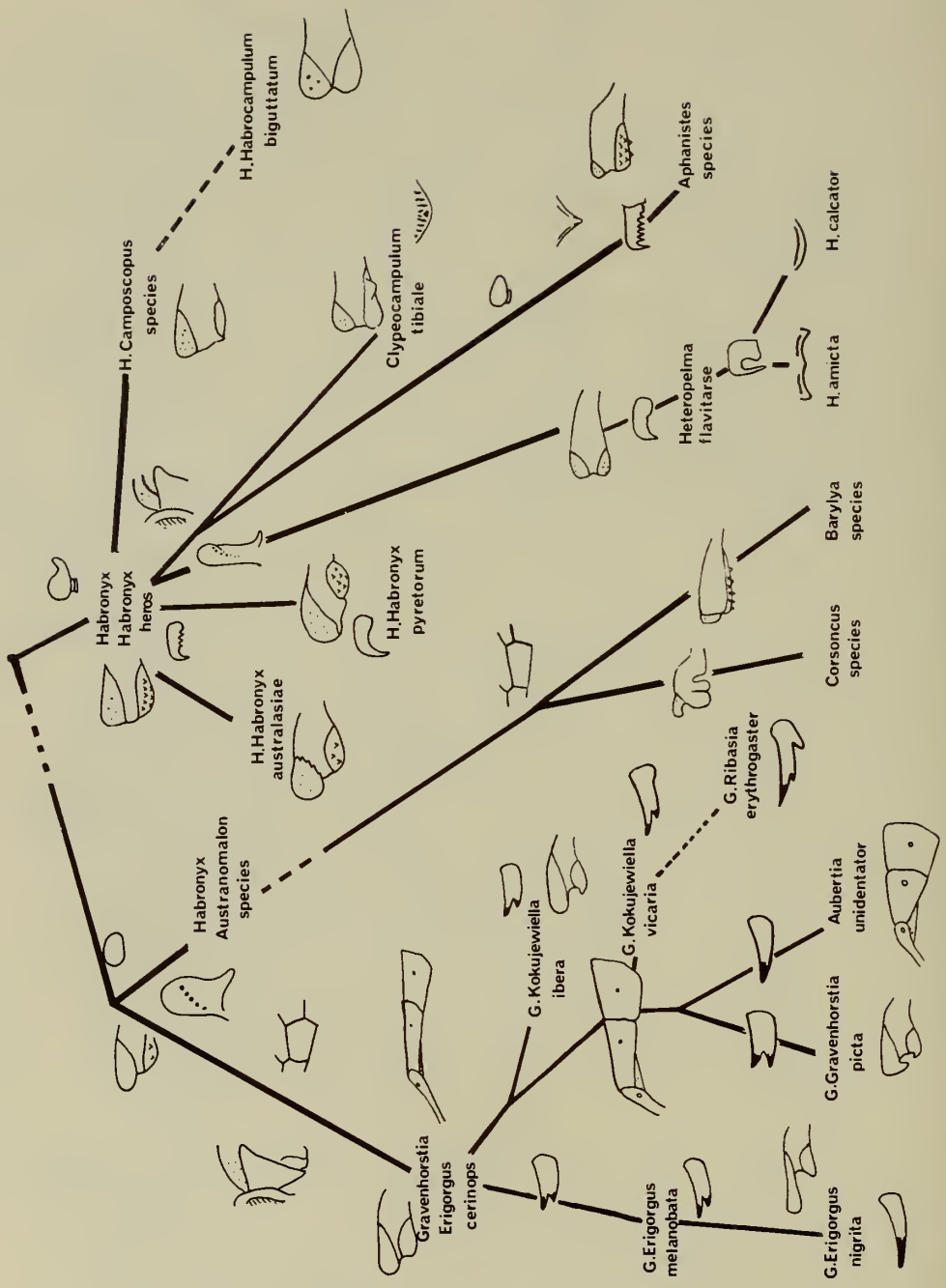
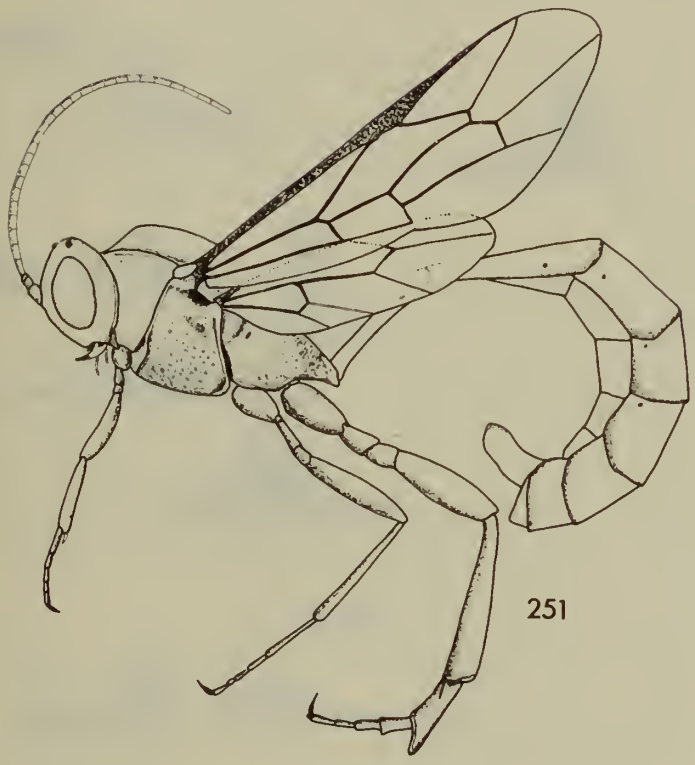
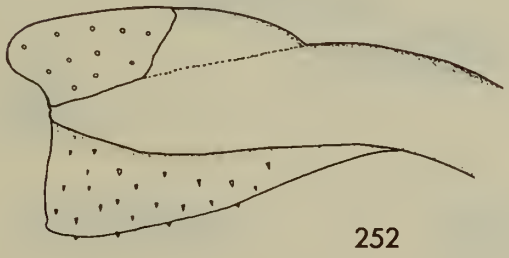


FIG. 250. Phylogenic interrelationships between the more primitive Therionine genera. Illustrations show the modifications that are thought to have occurred in the various evolutionary pathways. (For full discussion see text.)





FIGS 251, 252. *Porizonopteron metatarsator* Shaumar. 251, ♂ entire, lateral view; 252, aedeagus, lateral view.

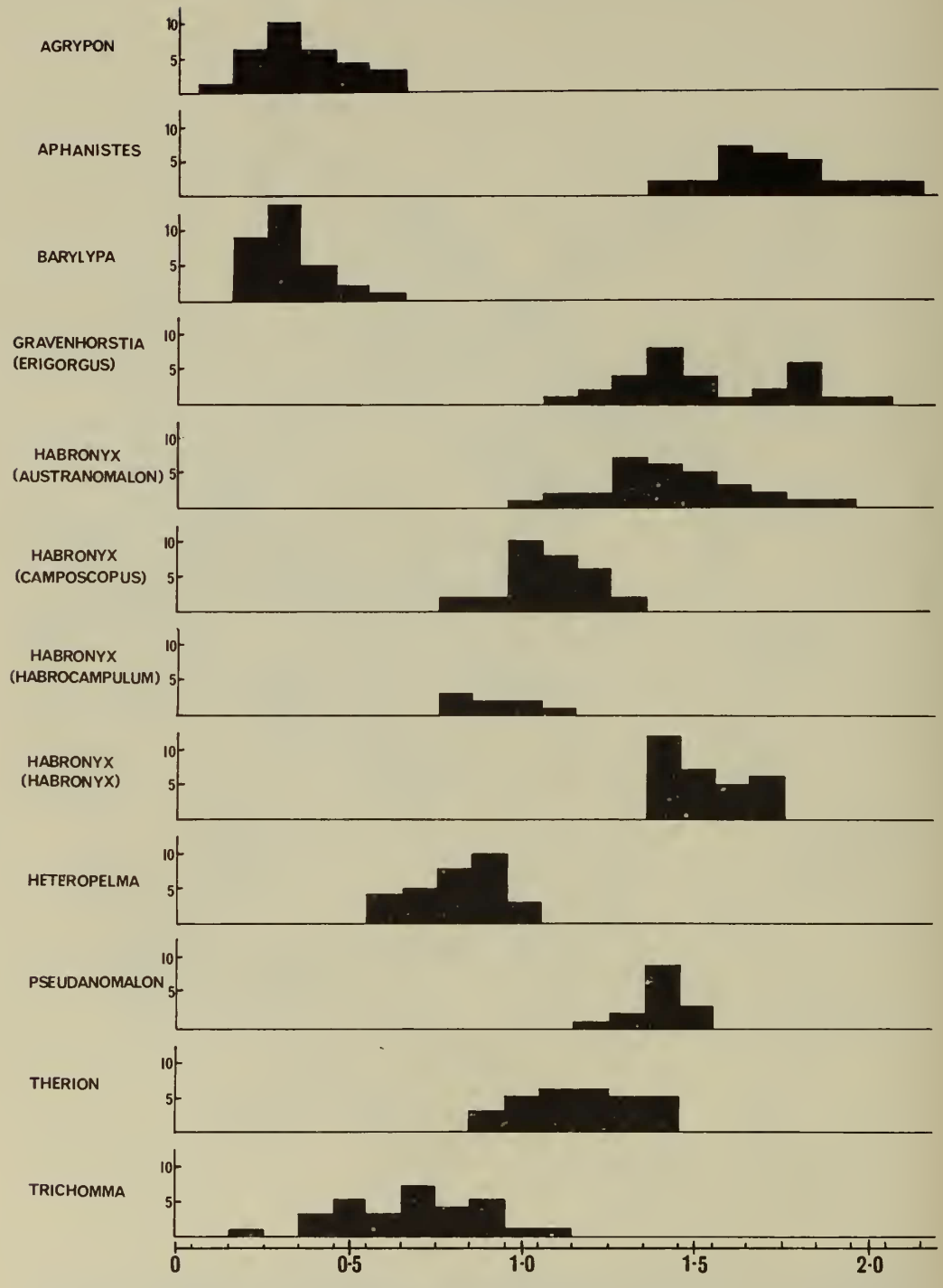


Chart 1. Comparison of the ranges of variation of the cubital index, CI, of the larger Therionine genera. x axis indicates values of CI; class width = 0·10: y axis indicates the number of individuals per class in each genus (n per genus = 30, except for *Habronyx* (*Habrocampulum*) n = 8 and *Pseudanomalon* n = 15).

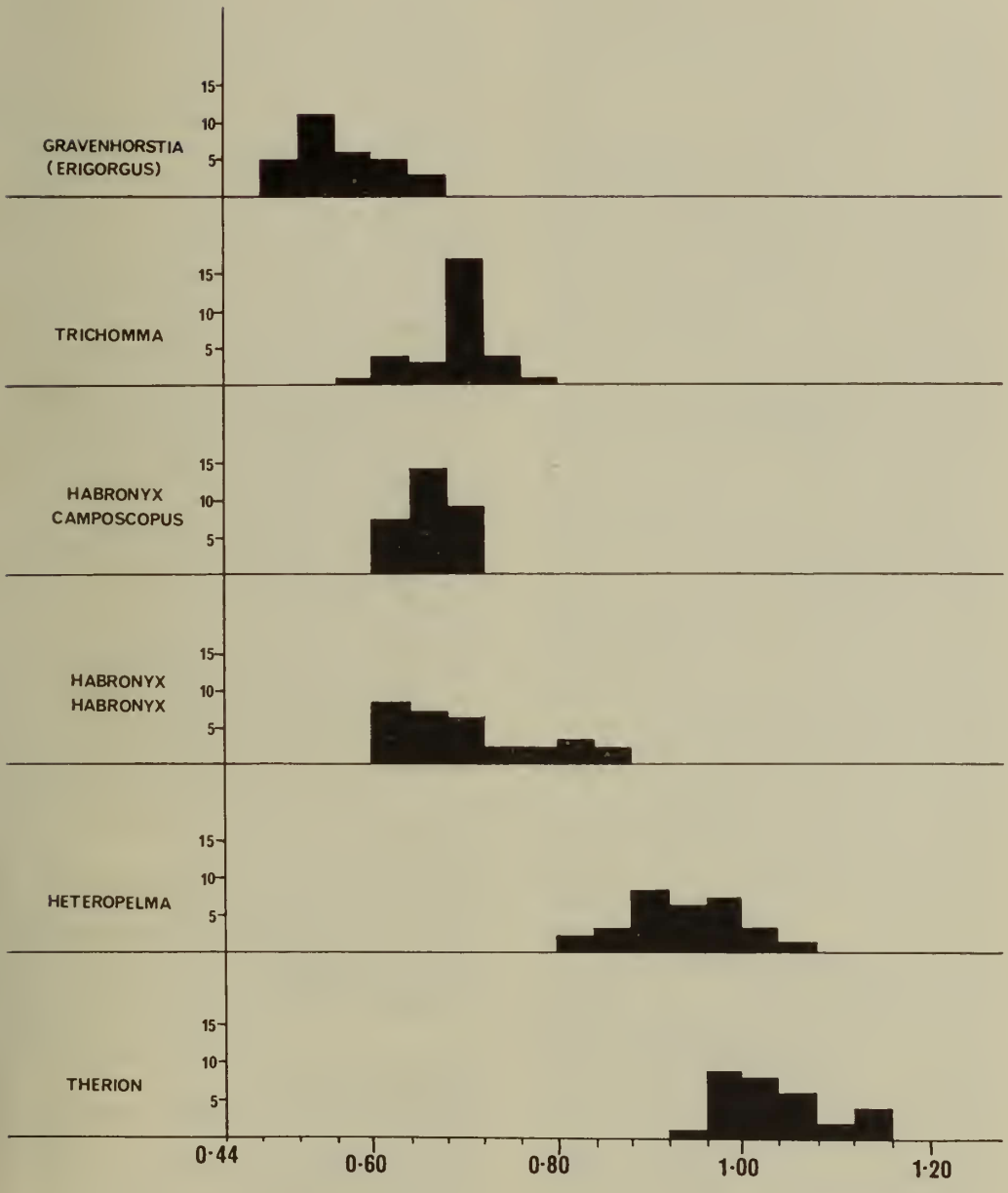


CHART 2. Comparison of the ranges of variation of the discobrachial index, DBI, of some Therionine genera. x axis indicates values of DBI; class width = 0·04: y axis indicates the number of individuals per class in each genus (n per genus = 30).

INDEX

Recognized synonyms are in *italics*; principal references are in **bold**.

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